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TAXONOMY OF *SPHAEROMERIA*, *ARTEMISIA*, AND *TANACETUM* (COMPOSITAE, ANTHEMIDEAE) BASED ON RANDOMLY AMPLIFIED POLYMORPHIC DNA (RAPD)

E. Durant McArthur[1], Renée Van Buren[2,3], Stewart C. Sanderson[1], and Kimball T. Harper[2]

ABSTRACT.—Relationships within, between, and among the Anthemideae genera *Sphaeromeria*, *Artemisia*, and *Tanacetum* were investigated using 238 randomly amplified polymorphic DNA (RAPD) markers obtained from twenty 10-mer primers amplified on genomic DNA. Forty-one populations from 16 taxa (15 species) were studied. Jaccard's coefficient of similarity and UPGMA clustering analysis were used to construct phenograms. *T* tests were used to make comparisons between samples at various systematic levels. DNA markers were 75% similar for conspecific populations. Sixteen *Sphaeromeria* populations (5 species) showed an average interspecific similarity of 21%. Interspecific similarity among 23 *Artemisia* populations (8 species with 2 subspecies of *A. tridentata* included) averaged 27%. Two *Tanacetum* species (1 population each) were 89% similar. The high similarity of the *Tanacetum* species was in the range of observed values for conspecific populations; indeed those 2 species (*T. vulgare* and *T. boreale*) have been considered conspecific by some authors. The 3 subgenera of *Artemisia* studied (*Artemisia*, *Dracunculus*, and *Tridentatae*) formed separate groups. In comparisons among the genera, *Sphaeromeria* was 18% similar to *Artemisia* (more similar to subgenus *Tridentatae* than the other *Artemisia* subgenera); intergeneric comparisons of *Sphaeromeria* and *Artemisia* and *Artemisia* and *Tanacetum* each were found to be 7% similar to each other. Thus, based on DNA markers, *Sphaeromeria* is more similar to *Artemisia* than it is to *Tanacetum*, which supports previously established morphological distinctions. *Sphaeromeria potentilloides* may be misplaced in the genus *Sphaeromeria* based on DNA marker results. It is likely that North American Anthemideae are circumboreal derivatives of ancestral Eurasian stock and that *Sphaeromeria* is derived from an *Artemisia*-like ancestor.

Key words: Sphaeromeria, Artemisia, Tanacetum, *Anthemideae, RAPD, taxonomy.*

Two decades ago Holmgren et al. (1976) published an intriguing article, "*Sphaeromeria*, a genus closer to *Artemisia* than to *Tanacetum* (Asteraceae: Anthemideae)." In their article Holmgren et al. (1976) returned *Sphaeromeria* to the generic rank first proposed by Nuttall (1841). Torrey and Gray (1843), however, reduced the taxon to subgeneric status (section *Sphaeromeria*) in the genus *Tanacetum*. *Sphaeromeria*, endemic to western North America (Holmgren et al. 1976, McArthur et al. 1989, Cronquist 1994), consists of 9 species, 8 of them rare. Several authors have noted that an understanding of relationships between and

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within the genera *Artemisia* and *Tanacetum* would be enhanced by new information on the distribution and phylogeny of that portion of the tribe Anthemideae (Hall and Clements 1923, Holmgren et al. 1976, McArthur 1979, McArthur et al. 1989).

Artemisia is the largest genus of Anthemideae, consisting of 250 or more species divided into 4 subgenera. It is distributed mostly in temperate portions of the northern hemisphere but also in South America and South Africa (Willis 1973, Bailey Hortorium Staff 1976, Greger 1978, McArthur 1979, McArthur et al. 1981, Ling 1995a). *Tanacetum* consists of some 50 species with a Eurasian distribution except for the *T. bipinnatum* complex, which is circumpolar (Willis 1973, Bailey Hortorium Staff 1976, McArthur 1979, Kyhos and Raven 1982). Here, we address relationships among the genera *Sphaeromeria*, *Artemisia*, and *Tanacetum* using genomic DNA markers from representative species from each genus. We also review species and generic distributions.

Randomly amplified polymorphic DNA (RAPD) analysis has been shown to be useful in studying plant population biology, in preparing genetic maps, and in classifying plants (Williams et al. 1990, 1993, Dawson et al. 1993, Russell et al. 1993, Williams and St. Clair 1993, Santos et al. 1994, Van Buren et al. 1994, Bradshaw et al. 1995, Gang and Weber 1995, Yeh et al. 1995, Bonnin et al. 1996, Karp et al. 1996, Lannér et al. 1996, Lin and Ritland 1996, Mudge et al. 1996, Smith et al. 1996, Stockinger et al. 1996). Whereas this paper examines similarity among related Anthemideae genera, a companion paper (McArthur et al. 1998) uses RAPD technology to examine hybridization and polyploidy within the subgenus *Tridentatae* of 1 of those genera (*Artemisia*). Our use of RAPD data to compare genera is novel but is, we believe, a natural extension of the many studies that have made population and species comparisons.

MATERIALS AND METHODS

Plant Materials

We identified and selected for study species representing morphological variation and geographical spread of the 3 genera of concern. Collecting sites for representative populations were determined for *Sphaeromeria* and *Artemisia* (Table 1), and representatives for *Tanacetum* were grown in our greenhouse from seed obtained from European colleagues (Table 1). We collected samples between May and August 1995, in most cases 3 populations (range 1–4) for each taxon. By combining tissue (young leaves) from 30 healthy but otherwise randomly chosen individuals of each population, we obtained a "bulked sample" for each population. Leaves were collected in nylon bags, immersed immediately in liquid nitrogen, and transported to the laboratory where they were stored at ultra-cold temperatures (−80°C) until DNA was extracted. Herbarium voucher specimens are deposited in the Shrub Sciences Laboratory (SSLP) or the Brigham Young University (BRY) herbaria. Following methods of McArthur and Sanderson (1985), we made a chromosome count from root tips of *Sphaeromeria diversifolia* to extend the cytological knowledge base in *Sphaeromeria* (several but not all *Sphaeromeria* species are cytologically known; Powell et al. 1974, Sanderson et al. 1984, McArthur et al. 1989).

DNA Extraction and Amplification

Bulked leaf samples were thoroughly mixed and a sample weighing 0.3–0.5 g from each population was used for DNA extraction. Extraction procedures generally followed Bult et al. (1992). This protocol resulted in high yields of genomic DNA ranging from approximately 100 μg/ml to nearly 400 μg/ml. DNA concentration was estimated using a Beckman DU 640 mass spectrophotometer (Beckman Instruments, Inc., Fullerton, CA). The extracted DNA was diluted with TE (1 M Tris and 0.5 M EDTA, pH 8.0) to achieve a final concentration of approximately 2.5 ng/μl.

Amplification of genomic DNA was accomplished following procedures reported by Williams et al. (1990). Amplification reactions with a final volume of 15 μl contained the following: 5–10 ng DNA, 1.5 μl 10X buffer, 100 μM each of 4 deoxynucleoside triphosphates (dATP, dCTP, dGTP, and dTTP), 3.5 mM $MgCl_2$, 0.4 μM primer (Operon Technologies, Inc., Alameda, CA), and 1.2 U Stoffel Fragment (Perkin Elmer-Cetus, Norwalk, CT). Amplification was carried out using a Perkin Elmer-Cetus DNA 48-well thermal cycler with the following cycling regime: (1) 3-min initiation step at 92°C; (2) 92°C for 1 min, 35°C for 1 min 45 sec, 72°C for 2 min, repeated for 45 cycles; and (3) 72°C for 7 min. Control reactions consisted of

Flora Societensis Stanley L. Welsh 8.5x11--420 pp.

This is a book for identification of the flowering plants of the Society Islands (Tahiti and adjacent islands). It contains keys to families, genera, and species, both indigenous and introduced. Some 105 families of dicots and 26 families of monocots are included. They contain 579 genera and 997 species. Short discussions follow each species description. A list of references, a glossary, a list of authors, and a complete index is included. Tahitian, French, and English names are included in the text and in the index.

The work, though technical, will aid interested lay and professional people in identification of most of the species encountered in these fascinating Islands.

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Flora Societensis

A Summary Revision of the Flowering Plants
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Mehetia, Tahiti, Moorea, Tetiaroa (îles du vent);
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Maupiti, and Mopelia (îles sous le vent)

Stanley L. Welsh, Ph.D.
Curator of the Herbarium
Brigham Young University
Provo, Utah 84602

TABLE 1. Location of sample collections and sample reference numbers.

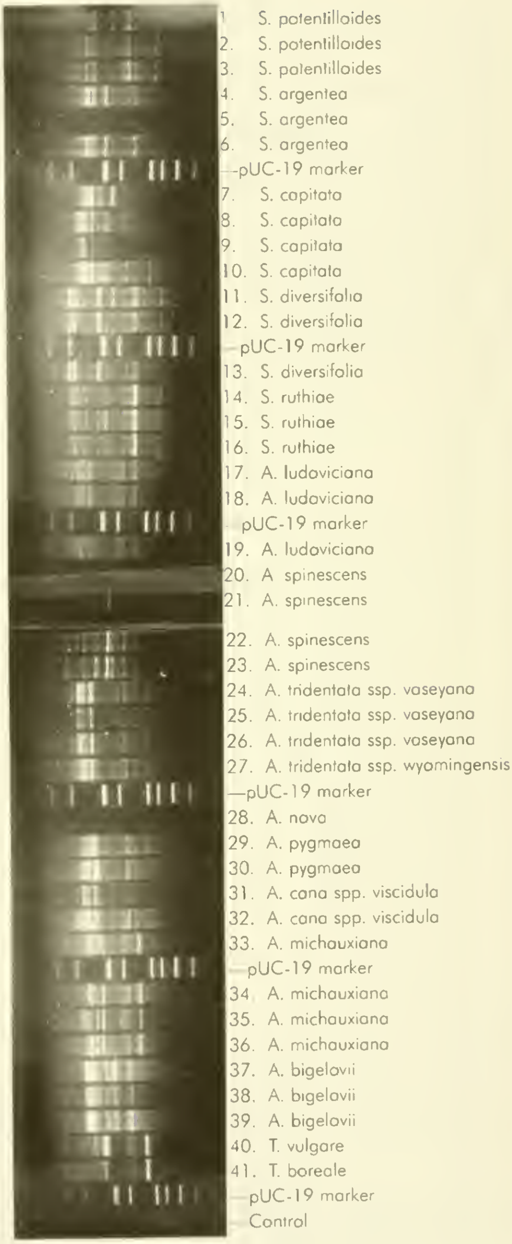
Collection	Location and sample reference number[a]
01. *Sphaeromeria potentilloides* (A. Gray) A.A. Heller	Hot Springs Hill, Eureka Co., NV, M&S 2428
02. *Sphaeromeria potentilloides* (A. Gray) A.A. Heller	4 km S of Hill City, Camas Co., ID, M&S 2425
03. *Sphaeromeria potentilloides* (A. Gray) A.A. Heller	1 km E of Reese River, U.S. Highway 50, Lander Co., NV, M&S 2427
04. *Sphaeromeria argentea* Nutt.	Point of Rocks, Sweetwater Co., WY, M&S 2422
05. *Sphaeromeria argentea* Nutt.	10 km SE of Mountain View, Uinta Co., WY, M&S 2424
06. *Sphaeromeria argentea* Nutt.	Near Opal, Lincoln Co., WY, H&V *s.n.*, 13 July 1995
07. *Sphaeromeria capitata* Nutt.	E Sevier Road, Bryce Canyon, Sevier Co., UT, H&V *s.n.*, 18 July 1995
08. *Sphaeromeria capitata* Nutt.	N of Lookout Mountain, Moffat Co., CO, M&S 2419
09. *Sphaeromeria capitata* Nutt.	Muddy Creek Bridge, Carbon Co., WY, M&S 2420
10. *Sphaeromeria capitata* Nutt.	I-80 exit 184, Sweetwater Co., WY, M&S 2421
11. *Sphaeromeria diversifolia* (D.C. Eat.) Rydb.	Rock Canyon, Utah Co., UT, H&V *s.n.*, 10 July 1995
12. *Sphaeromeria diversifolia* (D.C. Eat.) Rydb.	American Fork Canyon, Utah Co., UT, H&V *s.n.*, 10 July 1995
13. *Sphaeromeria diversifolia* (D.C. Eat.) Rydb.	Santaquin Canyon, Utah Co., UT, H&V *s.n.*, 10 July 1995 (also M&S 2041)
14. *Sphaeromeria ruthiae* Holmgren, Shultz, & Lowrey	Refrigerator Canyon, Zion National Park, Washington Co., UT, M,S,V,&Mu *s.n.*, 9 May 1995 (also M&S 1775)
15. *Sphaeromeria ruthiae* Holmgren, Shultz, & Lowrey	"The Barracks," E Fork Virgin River, Kane Co., UT, M,S,&Mu *s.n.*, 10 May 1995 (also M&S 1769)
16. *Sphaeromeria ruthiae* Holmgren, Shultz, & Lowrey	Pine Creek, Zion National Park, Washington Co., UT, M,S,&Mu *s.n.*, 10 May 1995 (also M&S 1774)
17. *Artemisia ludoviciana* Nutt.	"The Barracks," E Fork Virgin River, Kane Co., UT, M,S,&Mu 2393
18. *Artemisia ludoviciana* Nutt.	Salt Cave Hollow, Salt Creek Canyon, Juab Co., UT, M&S 2437
19. *Artemisia ludoviciana* Nutt.	Daniels Canyon, Wasatch Co., UT, M&S 2431
20. *Artemisia spinescens* D.C. Eaton	Middlegate, Churchill Co., NV, M&S *s.n.*, 6 June 1995
21. *Artemisia spinescens* D.C. Eaton	Desert Experimental Range, Millard Co., UT, H&V *s.n.*, 8 June 1995
22. *Artemisia spinescens* D.C. Eaton	S Pony Express trailhead, Faust, Tooele Co., UT, H&V *s.n.*, 5 June 1995
23. *Artemisia spinescens* D.C. Eaton	Secret Valley, Mono Co., CA, M&S *s.n.*, 10 June 1995
24. *Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle	Hobble Creek Canyon, Utah Co., UT, G,W,M,&L 21492
25. *Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle	Red Creek, Salina Canyon, Sevier Co., UT, M&S 2149
26. *Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle	Pine Valley, Washington Co., UT, M&S 2177
27. *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young	5 km W of junction of Faust Road and Utah Highway 73, Tooele Co., UT, H&V *s.n.*, 16 August 1995
28. *Artemisia nova* A. Nelson	3 km E of Faust, Tooele Co., UT, H&V *s.n.*, 16 August 1995
29. *Artemisia pygmaea* A. Gray	3 km E of Faust, Tooele Co., UT, H&V *s.n.*, 16 August 1995
30. *Artemisia pygmaea* A. Gray	E Sevier Road, Bryce Canyon, Sevier Co., UT, H&V *s.n.*, 18 July 1995
31. *Artemisia cana* Pursh. ssp. *viscidula* (Osterhout) Beetle	Daniels Summit, Wasatch Co., Utah, M&S 2430
32. *Artemisia cana* Pursh. ssp. *viscidula* (Osterhout) Beetle	Warner Pass, Lake Co., OR, M&S 2436
33. *Artemisia michauxiana* Besser	Snowbird, Little Cottonwood Canyon, Salt Lake Co., UT, H&V *s.n.*, 11 August 1995
34. *Artemisia michauxiana* Besser	Above Kingston, Lander Co., NV, M&S 2429
35. *Artemisia michauxiana* Besser	Lamoille Canyon, Ruby Range, Elko Co., NV, M&S 2426
36. *Artemisia michauxiana* Besser	Snowbird, Little Cottonwood Canyon, Salt Lake Co., UT, H&V *s.n.*, 11 August 1995 (1.5 km from 33)
37. *Artemisia bigelovii* A. Gray	Utah Highway 12, Milepost 36, Garfield Co., UT, H&V *s.n.*, 18 July 1995
38. *Artemisia bigelovii* A. Gray	Utah Highway 12, Milepost 51, Garfield Co., UT, H&V *s.n.*, 18 July 1995
39. *Artemisia bigelovii* A. Gray	North Creek Road, Garfield Co., UT, H&V *s.n.*, 18 July 1995
40. *Tanacetum vulgare* L.	Greenhouse grown from Bonn Botanical Garden, native population from Nordrhein-Westfalen, Eifel, Blankenheimerdorf, Germany 0613
41. *Tanacetum boreale* Fisch. ex. DC.	Greenhouse grown from Brunn, Czech Republic, Hortus Centralis Cultura Herbarum Mediicarum Facultas, Medica, Universitas, Masarykiana 770 (native population site unknown)

[a] Initials for the collectors are G = Sherel Goodrich, L = Mont E. Lewis, H = Kimball T Harper, M = E. Durant McArthur, Mu = Joanne Mudge, S= Stewart C. Sanderson, V = Renée Van Buren, and W = Alma H. Winward.

all reagents except DNA to identify ambiguous markers. Amplified products were separated and visualized using metaphore/agarose gel electrophoresis. DNA was stained with ethidium bromide and bands were photographed under UV light. Amplified bands were scored from photographs and recorded as presence or absence of bands of the same molecular weight (Fig. 1). The DNA size marker pUC-19 207 (Biosynthesis, Inc., Lewisville, TX) was added every 7th lane for reference and ease in scoring gels. A control lane (included all reagents but DNA) was also included (Fig. 1).

Analysis of Amplified DNA Products

We used the NTSYS-pc (version 1.80) statistical software package to analyze amplified DNA products (Rohlf 1993). Presence or absence of specific DNA bands (markers) was analyzed for percent similarity. To produce a similarity coefficient matrix for all samples in the analysis, we used Jaccard's coefficient of similarity (Jaccard 1912). UPGMA clustering analysis (NTSYS-pc, SAHN) was used to graphically show similarity among samples. A phenetic tree (NTSYS-pc, TREE) was generated to display percent similarity relationships among samples. Mean similarity values (with the standard deviations for each) were calculated for populations of each species, each genus, and among the 3 genera. For making comparisons of means within and between genera, species (and subspecies) population means were used. Many of these means were compared using *t* tests (Woolf 1968). Percentage values were arcsin transformed for statistical analyses but were converted back to percent values for reporting.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3. S. potentilloides
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5. S. argentea
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7. S. capitata
8. S. capitata
9. S. capitata
10. S. capitata
11. S. diversifolia
12. S. diversifolia
—pUC-19 marker
13. S. diversifolia
14. S. ruthiae
15. S. ruthiae
16. S. ruthiae
17. A. ludoviciana
18. A. ludoviciana
—pUC-19 marker
19. A. ludoviciana
20. A. spinescens
21. A. spinescens
22. A. spinescens
23. A. spinescens
24. A. tridentata ssp. vaseyana
25. A. tridentata ssp. vaseyana
26. A. tridentata ssp. vaseyana
27. A. tridentata ssp. wyomingensis
—pUC-19 marker
28. A. nova
29. A. pygmaea
30. A. pygmaea
31. A. cana spp. viscidula
32. A. cana spp. viscidula
33. A. michauxiana
—pUC-19 marker
34. A. michauxiana
35. A. michauxiana
36. A. michauxiana
37. A. bigelovii
38. A. bigelovii
39. A. bigelovii
40. T. vulgare
41. T. boreale
—pUC-19 marker
—Control

Fig. 1. Photograph of gel OPAW-19. Populations and taxa are identified to the right of each lane (the numbers refer to populations of Table 1). Molecular marker lanes (pUC-19 207) and a blank control lane are also labeled to the right.

RESULTS

Twenty primers (Table 2) produced 238 informative, scorable markers that were used to determine similarity among the selected *Sphaeromeria*, *Artemisia*, and *Tanacetum* taxa. Presence and absence data were used to compute percent similarity and to generate a phenogram (Fig. 2). The phenogram clearly distinguishes among the 3 genera of interest with the exception of a group at the top of the figure in which *Sphaeromeria potentilloides* and *Artemisia spinescens* are grouped. The phenogram (Fig. 2) also strongly groups the populations of each taxon. Percent similarity among populations of a single taxon, among species within a genus, and among the 3 genera of interest is reported in Tables 3 and 4.

TABLE 2. Primer name, sequence, and number of markers generated from each primer used for amplification of sample DNA.

Primer name[a]	Primer sequence (5′→3′)	Number of markers
OPAT-03	GACTGGGAGC	13
OPAT-04	TTGCCTCGCC	11
OPAT-06	CCGTCCCTGA	13
OPAT-08	TCCTCGTGGG	10
OPAT-11	CCAGATCTCC	11
OPAT-12	CTGCCTAGCC	15
OPAT-13	CTGGTGGAAG	10
OPAT-14	GTGCCGCACT	13
OPAT-15	TGACGCACGG	14
OPAT-17	AGCGACTGCT	10
OPAT-18	CCAGCTGTGA	13
OPAT-19	ACCAAGGCAC	9
OPAU-03	ACGAAACGGG	10
OPAU-04	GGCTTCTGTC	9
OPAU-07	AGACCCTTGG	9
OPAU-09	ACGGCCAATC	15
OPAU-11	CTTCTCGGTC	12
OPAU-15	TGCTGACGAC	16
OPAW-19	GGACACAGAG	14
OPAX-09	GGAAGTCCTG	11
TOTAL NUMBER OF MARKERS		238

[a] Operon Technologies, Inc., Alameda, CA

Tables 5 and 6, respectively, report similarities among the species of *Sphaeromeria* and *Artemisia*. Values in Tables 3 and 4 are the percent similarity to be expected for groups of plants at various levels of classification in the tribe Anthemideae. A full data matrix is available upon request from the senior author.

The chromosome number for *S. diversifolia* from Santaquin Canyon, Utah (McArthur & Sanderson 2041), is 2n = 18, the same number (as n = 9 or 2n = 18) for all other reported *Sphaeromeria* species [*S. cana* as *Tanacetum canum*, *S. nuttallii* as *T. nuttallii*, *S. potentilloides* as *T. potentilloides*, and *S. argentea* as *T. argentea* (Powell et al. 1974), and *S. argentea* (Sanderson et al. 1984) and *S. ruthiae* (McArthur et al. 1989)].

DISCUSSION

Inferences from RAPD Data

INTERPOPULATION SIMILARITY.—Within the genera *Sphaeromeria* and *Artemisia*, interpopulation similarity is 72.4 ± 2.3% (*s*) (Table 3). This is a reasonable value for populations of the same species using our system of analysis. Van Buren et al. (1994) reported about 80% similarity among populations of buttercups (*Ranunculus* spp.), Gang and Weber (1995) reported approximately 70% similarity among populations of white-stemmed rubber rabbitbrush (*Chrysothamnus nauseosus* ssp. *hololeucus*), and we found about 55% similarity in sagebrush (*Artemisia* subgenus *Tridentatae*) populations in a companion study (McArthur et al. 1998) using similar analytical techniques to those employed in this study. The patterns were similar for both genera: *Sphaeromeria* populations ranged from 53% to 85% similarity, *Artemisia* populations from 58% to 87% similarity.

SIMILARITY WITHIN GENERA.—Similarity of species within genera provided some instructive and interesting information (Table 4). The 5 species of *Sphaeromeria* were 20.7% similar and except for *S. potentilloides* clustered on the same stem of the phenogram (Fig. 2). When *S. potentilloides* is removed from the analysis, the mean congeneric percent similarity for *Sphaeromeria* is 24.7 ($n = 6$, $s = 6.5$). *Sphaeromeria potentilloides* has been recognized as somewhat distinct from other *Sphaeromeria* species by earlier workers (Holmgren et al. 1976, Cronquist 1994). Rydberg (1916) included *S. potentilloides* in the genus *Vesicarpa*, and Asa Gray included it in *Artemisia* but placed other currently recognized species of *Sphaeromeria* in *Tanacetum* (Torrey and Gray 1843, Holmgren et al. 1976). We compared the RAPD markers of the sampled *S. potentilloides* populations with all other *Sphaeromeria* populations by subjecting those values to a *t* test. Results indicate that *S. potentilloides* is no more similar to its congeners ($\bar{x} = 14.9\%$ similarity) than it is to the other populations ($\bar{x} = 15.4\%$ similarity) included in our study, $t = 0.27$, $p > 0.80$ (data not shown, but see Table 5 for comparison of means). It might be well to resurrect Rydberg's *Vesicarpa* for *S. potentilloides*. The relatively high RAPD marker similarity between *S. diversifolia* and *S. ruthiae* (Table 5) is consistent with their morphological and habitat preference similarities and with apparent volatile oil content (Holmgren et al. 1976, McArthur et al. 1989, unpublished).

The subgeneric taxonomy of *Artemisia* follows a tradition begun by Besser (1829) wherein he separated sections based on various combinations of disc and ray flower occurrences and fertility. Besser's 4 sections (*Abrotanum*, *Absinthium*, *Dracunculus*, *Seriphidium*) have, in the main, been retained. However, Rydberg (1916) elevated them to subgenera and created subordinate sections, and Poljakov (1961)

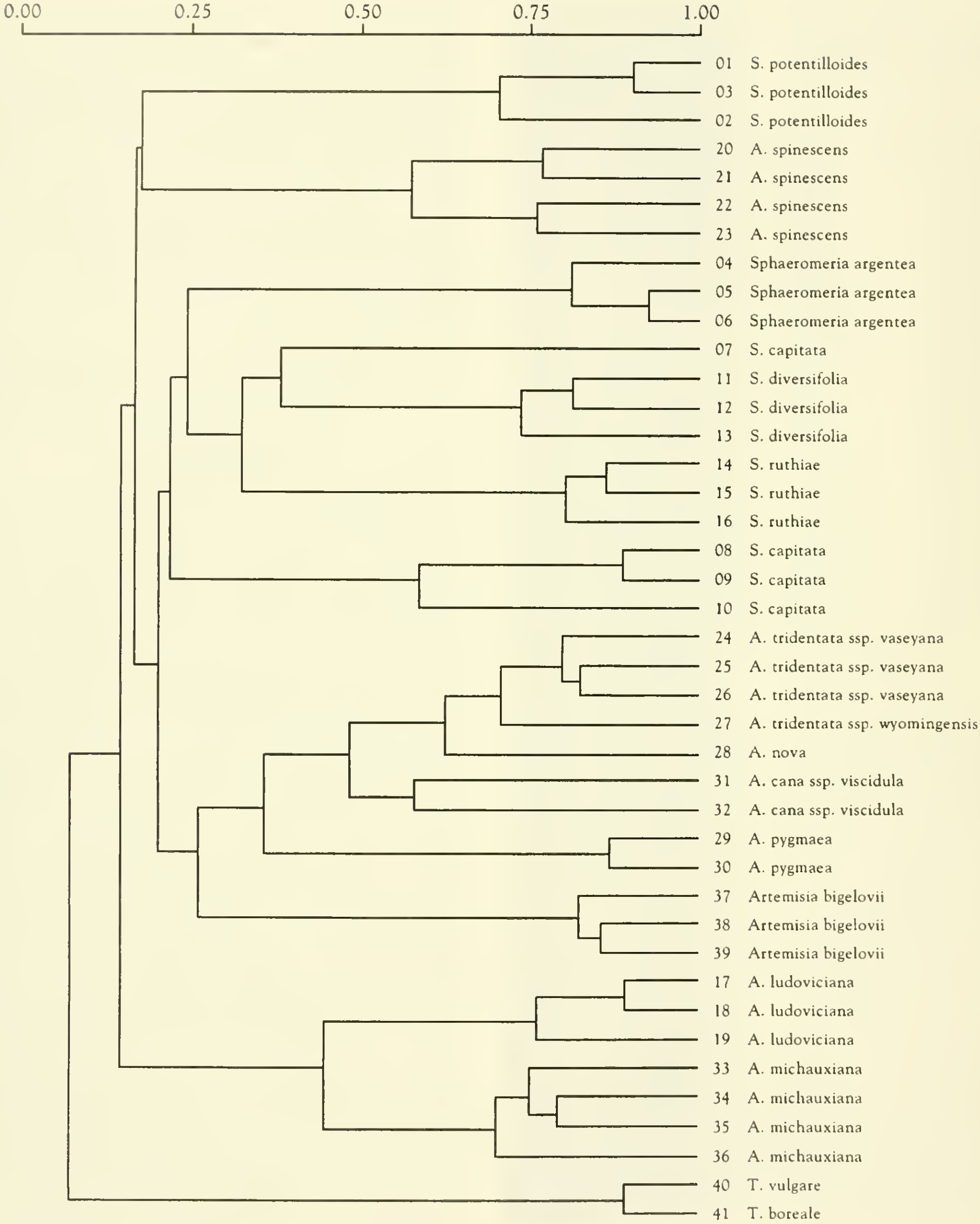

Fig. 2. Phenogram produced using Jaccard's coefficient of similarity and UPGMA clustering analysis (NTSYS-pc) for all 41 samples included in this study. Numbers preceding the species identify individual populations listed in Table 1.

united *Abrotanum* and *Absinthium* into the subgenus *Artemisia*. McArthur et al. (1981) separated Rydberg's section *Tridentatae* from the Eurasian subgenus *Seriphidium* based on karyotypic, chemotaxonomic, and distributional differences and recognized the section at the subgeneric level (see Persson 1974, McArthur and Plummer 1978, and McArthur 1979 for a more thorough review and references). Weber (1984) and Ling (1995b) consider *Tridentatae* a portion of *Seriphidium*. Seaman (1982) and Jeffrey (1995) support, as we do, the independence of *Tridentatae* from *Seriphidium*. We recognize 4 subgenera (*Artemisia*, *Dracunculus*,

TABLE 3. Mean percent similarity among populations.[a]

Interpopulation similarity	N^b	Mean	s
Sphaeromeria potentilloides	3	76.7	11.6
Sphaeromeria argentea	3	84.8	7.6
Sphaeromeria capitata	6	52.8	2.1
Sphaeromeria diversifolia	3	76.0	5.4
Sphaeromeria ruthiae	3	82.3	4.8
Artemisia ludoviciana	3	80.3	8.8
Artemisia michauxiana	6	73.1	3.9
Artemisia spinescens	6	63.5	12.8
Artemisia tridentata ssp. *vaseyana*	3	80.8	1.6
Artemisia cana ssp. *viscidula*	1	58.0	—
Artemisia pygmaea	1	87.0	—
Artemisia bigelovii	3	83.5	3.4
Mean interpopulational similarity	41	72.4	2.3
Mean within species	12	74.9	11.1

[a] Includes all species with more than 1 population sampled. See Table 1.

[b] N for each species is that of all comparisons, e.g., number of populations per species × number of populations per species minus 1 divided by 2. N for mean interpopulational similarity is the sum of species populations. N for mean within species is number of species.

TABLE 4. Mean percent similarity within and between genera.

	N^a	Mean	s
Similarity within a single genus			
Sphaeromeria	10	20.7	7.1
Artemisia	36	26.7	16.3
Tanacetum	1	88.9	—
Mean[b]	2	24.0	4.2
Similarity between genera			
Sphaeromeria/Artemisia	45	18.0	3.5
Sphaeromeria/Tanacetum	10	7.0	2.2
Artemisia/Tanacetum	18	7.0	2.5

[a] N for similarity within a single genus is the number of species (and subspecies) × number of species (and subspecies) minus 1 divided by 2. N for similarity between genera is the product of the number of species (and subspecies) in each genus.

[b] This mean includes only *Sphaeromeria* and *Artemisia* because *Tanacetum* species behaved as if they were populations of a single species and their sample number (2) was low.

Seriphidium, Tridentatae). Greger (1978) held a similar, if less formal, view. Representative species from the 3 subgenera that occur in North America (*Artemisia, Dracunculus, Tridentatae*) were included in this study.

The 8 species (9 taxa including 1 subspecies) of *Artemisia* included in this study are 26.7% similar (Table 3). *Artemisia* species cluster in 3 main stems in the phenogram (Fig. 2). Those stems correspond to the 3 subgenera to which the species belong. The only representative of subgenus *Dracunculus* included is *A. spinescens*. In our phenogram (Fig. 2) it clusters with *S. potentilloides* but at a relatively low coefficient of similarity. Nuttall (1841) originally placed *A. spinescens* in the monotypic genus *Picrothamnus*. The distant placement of *A. spinescens* from other *Artemisia* in the phenogram (Fig. 2) is in line with Bremer's (1994) statement that *Artemisia* is "known" to be a polyphyletic genus. Two subgenus *Artemisia* species were included, *A. ludoviciana* and *A. michauxiana*, and they form a rather tight group (Fig. 2, Table 6).

Six taxa (5 species) of the subgenus *Tridentatae* were included in this study: *A. tridentata* ssp. *vaseyana*, *A. t.* ssp. *wyomingensis*, *A. nova*, *A. cana* ssp. *viscidula*, *A. pygmaea*, and *A. bigelovii*. The latter 2 species have been considered questionable members of *Tridentatae*. Using various morphological, anatomical, chromosomal, and chemical criteria, Hall and Clements (1923), Moss (1940), Ward (1953), Beetle (1960), Hanks et al. (1973), McArthur et al. (1981), Shultz (1986), and Cronquist (1994) included *A. pygmaea* in *Tridentatae* (= North American *Seriphidium* of some treatments); whereas Holbo and Mozingo (1965) and Geissman and Irwin (1974) excluded it. Likewise, Moss (1940), Beetle (1960), Hanks et al. (1973), Geissman and Irwin (1974), and McArthur et al. (1981) included *A. bigelovii* in *Tridentatae*; Hall and Clements (1923), Ward (1953), Holbo and Mozingo (1965), Shultz (1986), and Cronquist (1994) excluded it. Both *A. pygmaea* and *A. bigelovii* can be included within *Tridentatae* based on RAPD data (Fig. 2, Table 6). Each taxon has more DNA marker similarity to some sister *Tridentatae* species than others, e.g., *A. bigelovii* with *A. pygmaea* and *A. cana* ssp. *viscidula; A. pygmaea* with *A. cana* ssp. *viscidula* and *A. tridentata* ssp. *vaseyana*. Our data do not support Beetle's (1960) suggestion that *A. nova* is most closely allied to *A. pygmaea*.

We subjected all *Tridentatae* taxa to t tests in which each was compared with other members of the group and with all non-*Tridentatae Artemisia* taxa in this study with respect to percentage similarity based on DNA markers. Results (data not shown) gave a mean percentage similarity of 40.5 ± 16.0 among species of *Tridentatae*. In contrast, species of the *Tridentatae* were only 16.1 ± 1.7% similar to non-*Tridentatae* taxa ($t = 6.7$, $p < 0.01$). A comparison of *A. spinescens* with other *Artemisia* species gave an average percent similarity of 15.6 ± 3.0.

TABLE 5. Interspecific similarity in the genus *Sphaeromeria*. Each value in the table is an average based on 9–12 independent comparisons. Similarity is based on RAPD markers.

Species[a] (N[b])	SPPO 3	SPAR 3	SPCA 4	SPDI 3	SPRU 3
S. potentilloides	—				
S. argentea	15.8	—			
S. capitata	16.4	24.5	—		
S. diversifolia	13.7	22.1	27.9	—	
S. ruthiae	13.3	22.3	15.9	35.3	—

[a] Species designations: SPPO = *Sphaeromeria potentilloides*, SPAR = *S. argentea*, SPCA = *S. capitata*, SPDI = *S. diversifolia*, SPRU = *S. ruthiae*.
[b] N = number of populations.

A similar comparison between the 2 subgenus *Artemisia* species (*A. ludoviciana* and *A. michauxiana*) and other *Artemisia* species gave a mean percent similarity of 15.0 ± 2.3. The 2 subgenus *Artemisia* species were 44.3% similar to each other (Table 6). These results and inspection of the values presented in Table 6 support the integrity of the subgenera as recognized herein, especially for subgenus *Tridentatae*, which was more thoroughly represented in the study than were the other subgenera.

Two *Tanacetum* species were sampled, *T. vulgare* and *T. boreale* (Table 1). By DNA marker analysis they were 88.9% similar (Fig. 2, Table 4), which is as similar as populations of the same species for the other taxa sampled in this study (Fig 2, Table 3) and as similar as conspecific populations in a similar study of portions of the genus *Ranunculus* (Van Buren et al. 1994). Both *Tanacetum* species are widely distributed in Eurasia, and *T. vulgare* is naturalized in temperate North America (Hultén and Fries 1986). Some, but not all, authors consider *T. boreale* mainly an Asian geographical variety of *T. vulgare* (Hultén and Fries 1986 and references in Goldblatt 1981, 1984, 1985, 1988 and Goldblatt and Johnson 1990, 1994). Our 2 study populations contrasted dramatically in leaf morphology (*T. vulgare* had much finer, pinnately dissected leaves). Unfortunately, we were unable to sample native North American *Tanacetum* material. However, all native North American species of *Tanacetum* are members of the hexaploid (n = 27) *T. bipinnatum* complex (Powell et al. 1974, Kyhos and Raven 1982), whereas numerous chromosome counts for *T. vulgare* and *T. boreale* have shown these taxa to be exclusively n = 9 diploids (Federov 1969, Goldblatt 1981, 1984, 1985, 1988, Goldblatt and Johnson 1990, 1994). As one goal of our research was to compare *Sphaeromeria* with *Tanacetum* and all known *Sphaeromeria* chromosome counts are diploid, n = 9 (Powell et al. 1974, McArthur et al. 1989), we think that comparisons made here among the *Sphaeromeria* and *Tanacetum* populations are appropriate and that lack of a comparison of the *T. bipinnatum* complex with *Sphaeromeria* is not a critical omission.

SIMILARITY BETWEEN GENERA.—The percent similarity of DNA markers between the genera of interest is given in Table 4 and Figure 2. These data support the established separation of the 3 genera. When the genera are compared (Table 4), the percent similarity between *Sphaeromeria* and *Artemisia* (18.0%) is greater than for other comparisons among these genera (7.0% similarity for both the *Sphaeromeria–Tanacetum* and the *Artemisia–Tanacetum* comparisons). These data are in full support of the Holmgren et al. (1976) conclusion that *Sphaeromeria* is more closely affiliated with *Artemisia* than with *Tanacetum*.

In the phenogram (Fig. 2), the top group consists of both *Sphaeromeria* and *Artemisia* samples; however, they share relatively little similarity with each other (<20%). In contrast, the major group of *Sphaeromeria*, the 2nd major stem of Figure 2, and the balance of the *Artemisia* samples, the 3rd and 4th major stems of Figure 2, cluster well above the 20% similarity level. That *S. potentilloides* and *A. spinescens* are on the same stem (Fig. 2) may reflect their uniqueness in regard to species within their own genera, as we have discussed in the previous section, rather than common phylogeny for those 2 taxa. The 3rd major stem of Figure 2 consists of samples of subgenus *Tridentatae*. This group is slightly more similar to the main *Sphaeromeria* stem than to other *Artemisia* and may therefore be an appropriate

TABLE 6. Interspecific similarity in the genus *Artemisia*. Each value in the table is an average based on 9–16 independent comparisons. Similarity is based on RAPD markers.

Species[a] (N^{b})	ARSP 4	ARLU 3	ARMI 4	ARTR^{V} 3	ARTR^{W} 1	ARCA^{V} 2	ARNO 1	ARPY 2	ARBI 3
ARSP	—								
ARLU	11.9	—							
ARMI	10.4	44.3	—						
ARTR^{V}	18.0	17.4	18.3	—					
ARTR^{W}	15.4	15.6	14.4	70.7	—				
ARCA^{V}	18.2	15.7	17.7	50.9	40.0	—			
ARNO	16.4	16.5	17.1	60.4	68.4	48.9	—		
ARPY	16.1	12.5	14.1	35.4	34.1	37.3	33.9	—	
ARBI	18.4	14.5	14.1	23.6	22.1	27.6	23.6	30.3	—

[a] Species designations: ARSP = *Artemisia spinescens*, ARLU = *A. ludoviciana*, ARMI = *A. michauxiana*, ARTR^{V} = *A. tridentata* ssp. *vaseyana*, ARTR^{W} = *A. t.* ssp. *wyomingensis*, ARCA^{V} = *A. cana* ssp. *viscidula*, ARNO = *A. nova*, ARPY = *A. pygmea*, ARBI = *A. biglovii*.

[b] N = number of populations.

place to look for the closest relatives of *Sphaeromeria*, although our expectation was that *Sphaeromeria* should be closer to the less woody *A. ludoviciana* complex.

ANTHEMIDEAE DISTRIBUTION AND PHYLOGENY

Anthemideae is one of the more morphologically and chemically specialized and phylogenetically advanced Compositae tribes (Cronquist 1955, Greger 1978, McArthur 1979, Zdero and Bohlmann 1990). Although the Compositae is one of the largest families of flowering plants, it became an important part of the earth's flora relatively late—in the mid-Tertiary (Raven and Axelrod 1974, Wagenitz 1976). Raven and Axelrod (1974) postulate an origin for the family in northern South America because the primitive generalized tribes Heliantheae and Mutisieae are concentrated there. Devore and Stuessy (1995) recently reviewed macromolecular data (cpDNA restriction site analysis, rbcL sequence data) that support a South American and southern hemisphere ancestry for the family. Regardless of its place of origin, however, the family rapidly, in geological terms, became established worldwide. Wagenitz (1976) suggested that the principal evolution and diversification in the family took place in xeric environments and in tropical mountains. In general, the family's migrations were achieved when the continents were close to their present positions (Raven and Axelrod 1974). The great Eurasian and North African landmass is the center of diversity for several tribes including Anthemideae (Bailey Hortorium Staff 1976, McArthur 1979). Of the principal Anthemideae genera, only *Artemisia*, *Achillea*, *Matricaria*, and *Tanacetum* have a natural North American distribution (Willis 1973, Bailey Hortorium Staff 1976, McArthur 1979). Of these 4 genera, *Artemisia* is by far the most common and diversified in North America. Each of these genera, including *Artemisia*, has circumpolar distributions with much stronger diversification in Eurasia than in North America. This information is consistent with our DNA marker data in suggesting that *Sphaeromeria* is a distinct genus aligned more closely with *Artemisia* than with other taxa.

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RANDOMLY AMPLIFIED POLYMORPHIC DNA ANALYSIS (RAPD) OF *ARTEMISIA* SUBGENUS *TRIDENTATAE* SPECIES AND HYBRIDS

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ABSTRACT.—Species of *Artemisia* (subgenus *Tridentatae*) dominate much of western North America. The genetic variation that allows this broad ecological adaptation is facilitated by hybridization and polyploidization. Three separate studies were performed in this group using randomly amplified polymorphic DNA (RAPD). Fifty-seven 10-mer primers generated nearly 400 markers from genomic DNA obtained from leaf tissue. These studies were (1) a measure of the variability of plants within and between populations and between subspecies using 5 *A. tridentata* ssp. *wyomingensis* populations, 2 *A. cana* ssp. *cana* populations, and 1 *A. cana* ssp. *viscidula* population; (2) an examination of the hypothesis that tetraploid (4*x*) *Artemisia tridentata* ssp. *vaseyana* derives *de novo* from diploid (2*x*) populations via autopolyploidy; and (3) an examination of the validity of the status of putative hybrids that have been produced by controlled pollination. These latter hybrid combinations—*A. tridentata* ssp. *tridentata* × *A. t.* ssp. *vaseyana*, *A. t.* ssp. *wyomingensis* × *A. tripartita*, and *A. cana* ssp. *cana* × *A. tridentata* ssp. *wyomingensis*—were made to combine traits of parental taxa in unique combinations with possible management application. RAPD marker data were subjected to similarity and UPGMA clustering analyses. RAPD markers were effective in measuring genetic diversity at different systematic levels. Individual plants within a population were approximately 55% to >80% similar to one another; populations within subspecies gave corresponding values of similarity, probably a result of the combined effects of large population sizes and wind pollination. The 2 subspecies of *A. cana* were approximately 45% similar. At least some 4*x* populations of *A. tridentata* ssp. *vaseyana* apparently derive *de novo* from 2*x* plants based on their being embedded in 2*x* phenogram groups, thus reinforcing evidence that autopolyploidy plays an important role in *Tridentatae* population biology. Two (*A. tridentata* ssp. *tridentata* × *A. t.* ssp. *vaseyana* and *A. cana* ssp. *cana* × *A. tridentata* ssp *wyomingensis*) of the 3 putative hybrid combinations were confirmed to include hybrids. These hybrids may have potential in management applications. Additional use of RAPD technology combined with other techniques may be useful in delimiting genetic characteristics and in guiding artificial selection in the *Tridentatae*.

Key words: Artemisia, Tridentatae, *RAPD, hybridization, diploid, tetraploid, polyploid, autopolyploidy.*

Subgenus *Tridentatae* of *Artemisia* is a group of plants centered on the landscape-dominant *A. tridentata* complex. There have been several treatments of this group, e.g., Rydberg 1916, Hall and Clements 1923, Ward 1953, Beetle 1960, Shultz 1986, Cronquist 1994; we recognize 11 species and 13 subspecies (McArthur and Plummer 1978, McArthur 1979, 1983, 1994, Goodrich et al. 1985, Rosentreter and Kelsey 1991, Winward and McArthur 1995). The *Tridentatae* are built upon polyploidization and hybridization (Ward 1953, Beetle 1960, Hanks et al. 1973, McArthur et al. 1979, 1981, 1988, Winward and McArthur 1995). Hybrid zones (see Harrison 1993 for summary and references) between subspecies of *A. tridentata* are yielding information about the nature, stability, and dynamics of these zones (McArthur et al. 1988, Freeman et al. 1991, 1995, Graham et al. 1995, Messina et al. 1996, Wang et al. 1997), an area of current interest among evolutionary biologists.

Randomly amplified polymorphic DNA analysis (RAPD) is yielding useful information about the population biology, classification, and genetic structure of plants (Williams et al. 1990, 1993, Fritsch et al. 1993, Levi et al. 1993, Santos et al. 1994, Van Buren et al. 1994, Bradshaw et al. 1995, Gang and Weber 1995, Yeh et al. 1995, Karp et al. 1996), including the nature and extent of natural and controlled hybridization (Huen and Helentjaris 1993, Bradshaw et al. 1994, Kennard et al. 1994, Dean and Arnold 1996, Lin and Ritland 1996, Mudge et al. 1996, Smith et al. 1996, Daehler and Strong 1997). This paper reports the use of genomic RAPD markers in better understanding the nature of population variation, polyploidy, and hybridization in the *Tridentatae* by reporting on the results of 3 studies: (1) DNA marker variation among populations of *A. tridentata* ssp. *wyomingensis* and between subspecies of *A. cana*; (2) DNA marker variation among diploid (2*x*) and tetraploid (4*x*) populations of *A. tridentata* ssp. *vaseyana* in addressing the possible *de novo* origin of 4*x* populations; and (3) DNA marker determination of the status of putative artificial hybrids, *A. tridentata* ssp. *tridentata* × *A. t.* ssp. *vaseyana*, *A. tridentata* ssp. *wyomingensis* × *A. tripartita*, and *A. cana* ssp. *cana* × *A. tridentata* ssp. *wyomingensis*. We have previously examined these problems using morphological characteristics (McArthur and Welch 1982, Freeman et al. 1991, 1995), chemistry (Hanks et al. 1973, Welch and McArthur 1981, Weber et al. 1994), and analyses integrating chemical and morphological approaches (McArthur et al. 1988, 1992, Graham et al. 1995, Messina et al. 1996, Wang et al. 1997). A companion paper addresses the use of RAPD analysis in the systematics of *Artemisia* and 2 sister genera, *Sphaeromeria* and *Tanacetum* (McArthur et al. 1998).

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MATERIALS AND METHODS

Plant Materials

Plant populations sampled and used in the 3 studies together with their taxonomic affiliation are listed in Table 1. We obtained these plant materials from the following: natural populations, samples of natural populations that had been propagated from seed in our greenhouse, outplantings of progeny from natural populations in experimental plots and common gardens, and putative artificial hybrids grown in the greenhouse and at outplanting sites. The putative hybrid seed was obtained using methods described previously (McArthur et al. 1979, 1988, Noller and McArthur 1986), i.e., placing inflorescences with dehiscing anthers in doubled pollination (white bakery) bags just before anthesis of the maternal parent. We removed pollination bags 3 wk later and collected seed before the heads shattered. Representative voucher samples for all 3 studies are deposited in the Shrub Sciences Laboratory Herbarium (SSLP). Leaves for DNA extraction and analysis were collected from individual plants during the 1991–92 growing season. We extracted DNA either from fresh material immediately after collection (<3 h) or from material that had been immediately frozen in liquid nitrogen and stored at ultra-cold temperatures (−80°C) until the tissue was extracted. DNA analysis was performed on individual plants and on bulked population samples (5–8 plants). Chromosome counts were made to assist in hybrid confirmation using the techniques described by McArthur and Sanderson (in review).

STUDY 1.—We examined DNA marker variability in populations at 2 different taxonomic levels (Table 1). First was the population level wherein we examined 5 different populations of *A. tridentata* ssp. *wyomingensis*. The 2nd level was between 2 subspecies of *A. cana* (2 populations of *A. cana* ssp. *cana* and 1 population of *A. c.* ssp. *viscidula*). We used both individual plants and bulked samples for DNA marker analysis.

STUDY 2.—We examined DNA markers from 7 *A. tridentata* ssp. *vaseyana* populations (Table 1, Fig. 1). Several locations where diploid (2*x*) and tetraploid (4*x*) populations of this taxon grow parapatrically or sympatrically have been discovered (McArthur and Sanderson in review). Some of those populations are included in this study (Table 1, Fig. 1). Initially, we thought the Hobble Creek location, which includes plants from both the mesic canyon bottom habitat and the more xeric south-facing slope habitat, included 2*x* and 4*x* populations. However, additional cytological study (McArthur and Sanderson in review, unpublished) has shown that the Hobble Creek location is essentially 2*x* with only an occasional 4*x* plant present. We kept the Hobble Creek population in the study for additional comparison of *A. tridentata* ssp. *vaseyana* DNA markers.

STUDY 3.—We examined DNA markers from 3 artificial hybridization experiments (Table 1). The 1st hybrid is *A. tridentata* ssp. *tridentata* × *A. t.* ssp. *vaseyana*, including F_1 and F_2 hybrid generations that have been studied and confirmed as hybrids in morphological, chemical, and insect-host contexts (Noller and McArthur 1986, McArthur et al. 1988, 1992, Weber et al. 1994, Messina et al. 1996, Richards, Messina, and McArthur unpublished). This hybrid combination was made in an attempt to better understand hybridization dynamics and combine traits (palatability, nutrient content, growth rates) that might be favorable for large herbivore

TABLE 1. Location of sample collections, outplanting sites, and sample reference numbers.

Taxon	Location and propagation information and sample reference number[a]
STUDY 1	
Artemisia tridentata Nutt. ssp. *wyomingensis* Beetle & Young	Arco, Butte Co., ID, W *s.n.*, October 1986; grown at Springville and Browns Park outplanting sites
	3 km S of Dinosaur, Rio Blanco Co., CO, M&S 1438; grown at Springville and Browns Park outplanting sites
	Gordon Creek, 7 km W of Spring Glenn, Carbon Co., UT, W U-019; grown at Springville and Browns Park outplanting sites
	6 km N of Kemmerer, Lincoln Co., WY, M&J 1738 (U-028); grown at Springville and Browns Park outplanting sites
	1 km E of Warren, Carbon Co., MT, M&J 1743; grown at Springville and Browns Park outplanting sites
Artemisia cana Pursh. ssp. *cana*	Maybell, Moffat Co., CO, M&S 2120; grown in Shrub Sciences Laboratory Greenhouse
	Sheridan, Sheridan Co., WY, Mo *s.n.*, 1972, M&S 2128; grown at the Snow Field Station
Artemisia cana Pursh. ssp. *viscidula* (Osterhout) Beetle	Cart Creek, Daggett Co., UT, M&B 2204
STUDY 2	
Artemisia tridentata Nutt. ssp. *vaseyana* (Rydb.) Beetle	Right Fork of Hobble Creek, Utah., UT, M&S 2184, 2185; grown at Hobble Creek and Great Basin Experimental Range outplanting sites, 2*x*
	4 km E of Salina Canyon Summit, Red Creek, Sevier Co., UT, M&S 2149; grown at Hobble Creek and Great Basin Experimental Range outplanting sites, 2*x*
	7 km E of Salina Canyon Summit, Red Creek, Sevier Co., UT, M&S 2148; grown at Hobble Creek and Great Basin Experimental Range outplanting sites, 4*x*
	Pine Valley, Washington Co., UT, M&S 2177; grown at Hobble Creek and Great Basin Experimental Range outplanting sites, 2*x*
	8 km N of St. George, E of Snows Canyon, Washington Co., UT, M&S 2189; grown at Hobble Creek and Great Basin Experimental Range outplanting sites, 4*x*
	Tabernacle Dome, Kolob Terrace, Zion National Park, Washington Co., UT, M&S 1821A; grown at Hobble Creek and Great Basin Experimental Range outplanting sites, 2*x*
	4 km N of Virgin, Washington Co., UT, M&S 2191; grown at Hobble Creek and Great Basin Experimental Range outplanting sites, 4*x*
STUDY 3	
Artemisia tridentata Nutt. ssp. *tridentata*	12 km E of Dove Creek, Delores Co., CO, M&P U-076, V&Ba 22; grown at Snow Field Station and Hobble Creek outplanting sites
Artemisia tridentata Nutt. ssp. *vaseyana* (Rydb.) Beetle	Hobble Creek Canyon, Utah Co., UT, M&P U-001, M&S 1476, 2144, 2363, G,Wi,M,L 21492; grown at Hobble Creek outplanting sites
Artemisia cana Pursh. ssp. *cana*	Sheridan, Sheridan Co., WY, Mo *s.n.*, 1972, M&S 2128; grown at the Snow Field Station
Artemisia tripartita Rydb.	West entrance, U.S. Sheep Station, Dubois, Clark Co., ID; M&S 2082
	Paddock 31A, U.S. Sheep Station, Dubois, Clark Co., ID; M&S *s.n.*, August 1994
Artemisia tridentata Nutt. ssp. *wyomingensis* Beetle & Young	Arco, Butte Co., ID, W *s.n.*, October 1986; grown at Springville and Browns Park outplanting sites
	6 km N of Kemmerer, Lincoln Co., WY, M&J 1738 (U-028); grown at Springville and Browns Park outplanting sites

[a] Initials for collectors are B = David G. Babbel, Ba = Jerry R. Barker, G = Sherel Goodrich, J = Gary L. Jorgensen, L = Mont E. Lewis, M = E. Durant McArthur, Mo = Stephen B. Monsen, P = A. Perry Plummer, S = Stewart C. Sanderson, V = Gordon A. Van Epps, W = Bruce L. Welch, and Wi = Alma H. Winward. The U collection numbers refer to seed and plant culture accession numbers maintained at the Great Basin Experimental Range, Ephraim, UT. For locations of the outplanting sites see Figure 1

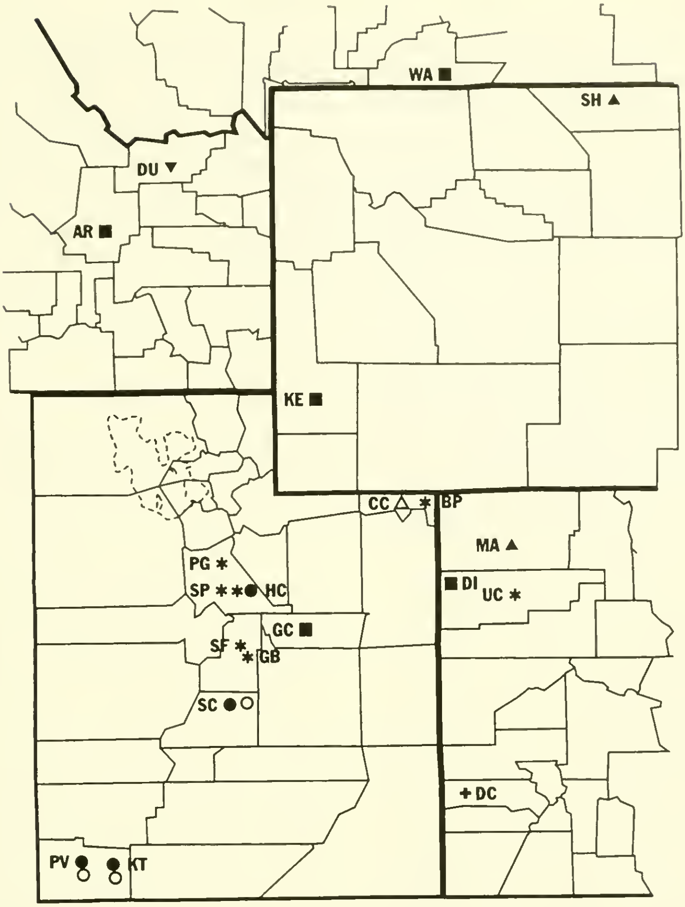


Fig. 1. Locations of plant population native sites and of outplanting sites. See Table 1 for more detail. ✱ = outplanting sites, BP = Browns Park (Bureau of Land Management), GB = Great Basin Experimental Range (Rocky Mountain Research Station and Manti–La Sal National Forest), HC = Hobble Creek (Utah Division of Wildlife Resources), PG = Pleasant Grove (Uinta National Forest), SF = Snow Field Station (Rocky Mountain Research Station, Division of Wildlife Resources, Snow College, and Utah State University Agricultural Experiment Station), SP = Springville (Utah Division of Wildlife Resources), UC = Upper Colorado Environmental Plant Center (Natural Resources Conservation Service and Douglas and White River Soil Conservation Districts); ● = 2*x* *Artemisia tridentata* ssp. *vaseyana*, HC = Hobble Creek (M&P U-001, G,Wi,M,&L 21492, M&S 2184, 2185), KT = Kolob Terrace (M&S 1821A), PV = Pine Valley (M&S 2177), SC = Salina Canyon (M&S 2149); ○ = 4*x* *A. t.* ssp. *vaseyana*, KT = Kolob Terrace (M&S 2191), PV = Pine Valley (M&S 2189), SC = Salina Canyon (M&S 2148); ■ = *Artemisia tridentata* ssp. *wyomingensis*, AR = Arco (W *s.n.*, Oct. 1986), DI = Dinosaur (M&S 1438), GC = Gordon Creek (W U-019), KE = Kemmerer (M&J 1738), WA = Warren (M&J 1743); ✚ = *Artemisia tridentata* ssp. *tridentata*, DC = Dove Creek (M&P U-076); ▲ = *Artemisia cana* ssp. *cana*, MA = Maybell (M&S 2120), SH = Sheridan (Mo *s.n.*, 1972, M&S 2128); △ = *Artemisia cana* ssp. *viscidula*, CC = Cart Creek (M&B 2204); ▼ = *Artemisia tripartita*, DU = U.S. Sheep Station, Dubois (M&S 2082, *s.n.*, Aug. 1994).

consumption (McArthur et al. 1988, 1992, Weber et al. 1994). The 2nd putative hybrid combination is *A. t.* ssp. *wyomingensis* × *A. tripartita* (4 different combinations involving the Warren, Montana, and Gordon Creek, Utah, populations of *A. tridentata* ssp. *wyomingensis* as female parents and 2 *A. tripartita* populations from the entry snow fence and paddock 31A of the U.S. Sheep Station, Dubois, Idaho, as pollen donors). The 3rd combination is *A. cana* ssp. *cana* × *A. tridentata* ssp. *wyomingensis* (3 combinations with *A. c.* ssp. *cana* from Sheridan, Wyoming, as the female parent and *A. t.* ssp. *wyomingensis* from Arco, Idaho, and Kemmerer, Wyoming, as pollen donors). These latter 2 putative hybrid combinations were designed to attempt to combine the drought tolerance of *A. t.* ssp. *wyomingensis* with the root-sprouting, fire-tolerant adaptation of *A. c.* ssp. *cana* and *A. tripartita* (McArthur et al. 1992, McArthur 1994). *Artemisia tridentata* ssp. *wyomingensis* is not fire tolerant, and much of its range has been usurped by alien fire-adapted weed species such as *Bromus tectorum* (McArthur et al. 1990, Monsen and Kitchen 1994).

DNA Extraction and Amplification

We extracted DNA from individual plants or bulked samples using a method adapted from Delaporta et al. (1983). After the tissue was ground to a powder in liquid nitrogen using a mortar and pestle, about 1–1.5 ml extraction buffer (10 mM EDTA, pH 8.00; 50 mM NaCl, 100 μL 20% SDS and 5 μ 2 β mercaptoethanol) per gram of plant tissue was added and the mixture ground further. One-ml portions of the homogenate were transferred to 1.5-ml centrifuge tubes and incubated for 20 min at 68°C in a water bath. Following incubation, 500 μL of 1 M potassium acetate was added to each tube and the tubes mixed thoroughly. We then incubated the samples at 4°C for 20 min. Following incubation, the samples were centrifuged at 14,000 rpm for 5 min. The supernatant was transferred through micracloth to a clean microcentrifuge tube containing 500 μL of isopropanol. The tubes were mixed by gently inverting and the samples incubated overnight at 4°C to help precipitate the DNA (Fairbanks et al. 1993).

Because of the high amount of carbohydrate obtained after the above extraction, we performed a carbohydrate wash (Sederhof, North Carolina State University, Chapel Hill, personal communication). All tubes containing DNA from a particular plant or bulked sample were combined to form single pellets. Each pellet was resuspended in 700 μL of 1 M NaCl and vortexed gently (DNA dissolves in the salt but carbohydrates do not). The samples were incubated at 4°C for 20 min and then centrifuged at 14,000 rpm for ca 5 min. The resulting supernatant was added 1:1 to isopropanol and incubated overnight at 4°C to aid DNA precipitation. The DNA was pelleted and washed with 70% ethanol, dissolved in TE (10 mM Tris, pH 8.00; 1 mM EDTA, pH 8.0), and stored at –20°C until use.

DNA markers were amplified with either AmpliTaq DNA Polymerase or AmpliTaq DNA Polymerase Stoffel Fragment (Perkin Elmer-Cetus, Norwalk, CT). Both enzymes were used to obtain different DNA bands with the same primer because AmpliTaq tended to amplify higher molecular weight markers than did Stoffel Fragment (Sobral and Honeycutt 1993). Amplifications were performed according to Williams et al. (1990) as modified by Mudge et al. (1996). Reagents for RAPD amplification were obtained from Perkin Elmer-Cetus and Promega Corp. (Madison, WI), primers from Operon Technologies, Inc. (Alameda, CA) and the University of British Columbia Biotechnology Laboratory (Vancouver, BC). The reaction preparation was automated by means of a Biomek 1000 work station (Beckman Instruments Inc., Fullerton, CA). Each sample for amplification had a total volume of 15 μL. Amplifications were carried out on 3 MJ Research PTC-100 96-well thermocyclers (MJ Research Inc., Watertown, MA) with different programs for AmpliTaq and Stoffel Fragment. The AmpliTaq program consisted of an initial denaturation step at 92°C for 3 min, followed by 48 cycles of denaturation step at 86°C for 1 min, 36°C for 1 min 45 sec, and 72°C for 2 min. Once the 48 cycles were complete, samples were held at 72°C for 7 min and then stored at 4°C until electrophoresis. Minimum ramp times were used between each step. The Stoffel Fragment program consisted of an initial denaturation step at 94°C for 3 min followed by 40 cycles of 96°C for 1 sec, a 0.5°C s^{-1} ramp to 35°C which was held for 1 sec, a 0.3°C s^{-1} ramp to 72°C which was held for 1 sec, and a 0.2°C s^{-1} ramp to 96°C. Once the 40 cycles were complete, samples were held at 72°C for 7 min and then stored at 4°C until electrophoresis.

DNA amplification products were separated by electrophoresis in 20 × 25- or 20 × 40-cm 20 g L^{-1} 1:4 Low (2%) EEO agarose: FMC Metaphor (FMC Bioproducts, Rockland, ME) gels with up to 28 lanes. The entire 15-μL sample plus 2–3 μL of bromophenol blue dye in glycerol was added to each lane. DNA size markers (pUC-19 207, Biosynthesis, Inc., Lewisville, TX) were added to at least 2 lanes in each gel for reference and ease in scoring gels. Samples were electrophoresced at 150 V for 3 to 4 h at room temperature.

Gels were stained with 0.5 μg ethidium bromide per ml in both gel and gel buffer. They were not destained. Gels were visualized on a UV transilluminator and photographed with a camera system, or they were viewed on a video imaging system that had greater resolution and storage capabilities than photographic methods have (Mudge et al. 1996). Amplified bands were scored and recorded as presence or absence of bands of the same molecular weight (Fig. 2). Bands of the same mobility were presumed to be homologous.

Analysis of Amplified DNA Products

The NTSYS-pc statistical software package was used to analyze coded DNA markers (Rohlf 1993). Presence or absence of specific DNA bands (markers) was analyzed for estimating percent similarity with Jaccard's coefficient of similarity (Jaccard 1912) using NTSYS-pc, version 1.80. UPGMA clustering analysis (NTSYS-pc, SAHN) and a phenetic tree (NTSYS-pc, TREE) were generated to graphically show the percent similarity among appropriate samples. Phenetic trees were constructed from individual plant data except for the *Artemisia tridentata* ssp. *wyomingensis* population study. In that study both individual plant and bulked data were used. The bulked data were not weighted; i.e, they were treated analogously to a single plant. Bulked samples included 5–8 individual plants.

RESULTS

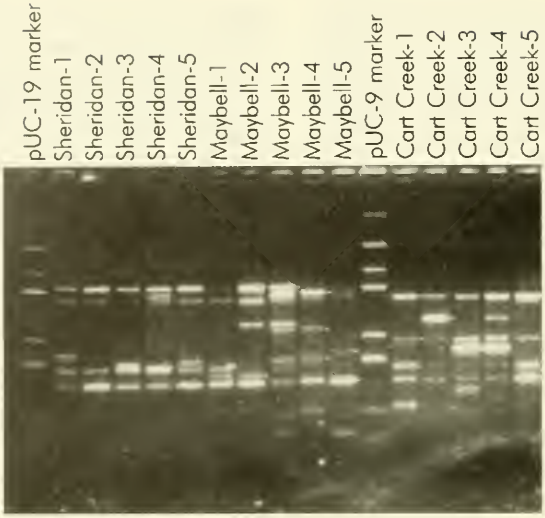
Fifty-seven primers (3–24 per study) produced nearly 400 (6–216 per study) scorable markers that were used to construct similarity phenograms (Tables 2, 3, Figs. 3–6). The primer and marker totals of Table 2 are not additive because 21 of the primers and as many as 150 of the DNA markers were shared between or among the separate studies.

STUDY 1.—Figures 3 and 4 show individual plant similarity within populations of *A. tridentata* ssp. *wyomingensis*, *A. cana* ssp. *cana*, and *A. c.* ssp. *viscidula*; among-population similarity within each taxon; and similarity between subspecies of *A. cana*. These results are within expected ranges at those systematic levels (Van Buren et al. 1994, Gang and Weber 1995, McArthur et al. 1998). Individual plants within each population are generally but not always more similar to other plants in their own population than plants of the same taxon in other populations.

The Gordon Creek, Utah, and Warren, Montana, populations of *A. tridentata* ssp. *wyomingensis* are less homogeneous than the other 3 populations of *A. t.* ssp. *wyomingensis* (Arco, Idaho; Kemmerer, Wyoming; Dinosaur, Colorado). Bulked samples show that the 3 geographically clustered populations (Dinosaur, Colorado; Gordon Creek, Utah; and Kemmerer, Wyoming) are slightly more similar to each another than to the more geographically isolated populations, Arco, Idaho, and especially Warren, Montana (Figs. 1, 3). Under the conditions of our study, individual plants within populations were approximately 55% to >80% similar in DNA markers. All populations are at least 50% similar to each other except for 1 outlying plant from Warren, Montana (Fig. 3).

The 2 populations of *A. cana* ssp. *cana* were about 54% similar to each other, whereas those populations were only 45% similar to the population of *A. cana* ssp. *viscidula* included in the study (Fig. 4). The Sheridan, Wyoming, population of *A. c.* ssp. *cana* and the Cart Creek, Utah, population of *A. c.* ssp. *viscidula* are more homogeneous than is the Maybell, Colorado, population of *A. c.* ssp. *cana*. The similarity between *A. cana* subspecies is supportive of their conspecific affinity and placement within the subgenus *Tridentatae* (McArthur et al. 1998).

STUDY 2.—Comparisons of the 2*x* and 4*x* populations of *A. tridentata* ssp. *vaseyana* are presented in the Figure 4 phenogram as individual plants. In general, as in study 1, individual plants for each population clustered on the same stem. All plants and populations for this subspecies were >50% similar as was the case for plants and populations within subspecies in study 1. Results reveal 4 groups with >55% similarity (Fig. 5): the top one comprises the 11 Salina Canyon (Utah) 2*x* plants, 16 of the 21 Hobble Creek (Utah) 2*x* plants, and 1 of the 11 Kolob Terrace (Utah) 4*x* plants; the 2nd group is composed of all 8 Pine Valley (Utah) 2*x* plants, all 12 Pine Valley 4*x* plants, and 11 of the 12 Kolob Terrace 2*x* plants; the 3rd one is composed of the 9 Salina Canyon 4*x* plants, 5 of the 21 Hobble Creek 2*x* plants, and 1 Kolob Terrace 4*x* plant; the bottom group comprises 9 of the 11 Kolob Terrace 4*x* plants and a single Kolob Terrace 2*x* plant. These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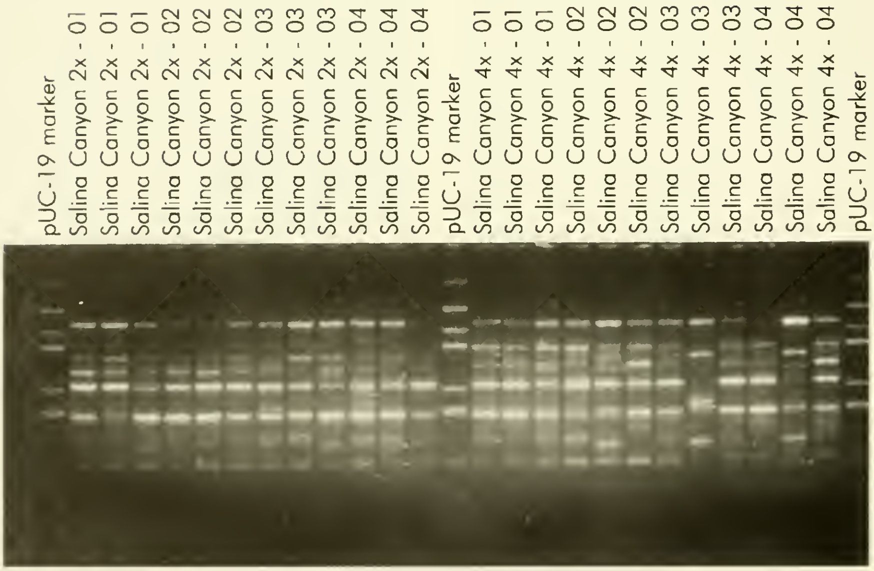
Sheridan-1
Sheridan-2
Sheridan-3
Sheridan-4
Sheridan-5
Maybell-1
Maybell-2
Maybell-3
Maybell-4
Maybell-5
pUC-9 marker
Cart Creek-1
Cart Creek-2
Cart Creek-3
Cart Creek-4
Cart Creek-5

Artemisia cana


pUC-19 marker
Salina Canyon 2x - 01
Salina Canyon 2x - 01
Salina Canyon 2x - 01
Salina Canyon 2x - 02
Salina Canyon 2x - 02
Salina Canyon 2x - 02
Salina Canyon 2x - 03
Salina Canyon 2x - 03
Salina Canyon 2x - 03
Salina Canyon 2x - 04
Salina Canyon 2x - 04
Salina Canyon 2x - 04
pUC-19 marker
Salina Canyon 4x - 01
Salina Canyon 4x - 01
Salina Canyon 4x - 01
Salina Canyon 4x - 02
Salina Canyon 4x - 02
Salina Canyon 4x - 02
Salina Canyon 4x - 03
Salina Canyon 4x - 03
Salina Canyon 4x - 03
Salina Canyon 4x - 04
Salina Canyon 4x - 04
Salina Canyon 4x - 04
pUC-19 marker

Artemisia tridentata ssp. vaseyana

Fig. 2. Photographs of gels: top, photograph of *Artemisia cana* subspecies (gel UBC 285); bottom, photograph of *Artemisia tridentata* ssp. *vaseyana* 2*x* and 4*x* populations from Salina Canyon (gel 598). Triplicate plant samples are in lanes labeled 01, 02, etc.; molecular marker lanes (pUC-19 207) are labeled.

results are consistent with geographic separation (Fig. 1) except for 2 Kolob Terrace 4*x* plants that are in the 1st and third groups, respectively, rather than the 4th group (Fig. 5). The 1st and 2nd groups, 55% similar, are 2*x* with the exception of the 4*x* Pine Valley plants and a single 4*x* Kolob Terrace plant, whereas the 3rd and 4th groups, 54% similar, are primarily

TABLE 2. Number of primers and DNA marker bands used in separate studies.

Study	No. of primers	No. of bands	Primer sources[a]
STUDY 1			
Artemisia tridentata ssp. *wyomingensis* populations	22[b]	149	Operon, UBC
Artemisia cana subspecies	24[c]	216	Operon, UBC
STUDY 2			
Artemisia tridentata ssp. *vaseyana*, 2*x* and 4*x*	14[d]	133	UBC
STUDY 3			
Artemisia tridentata ssp. *tridentata* × *A. t.* ssp. *vaseyana*	11[e]	19	Operon
Artemisia tridentata ssp. *wyomingensis* × *A. tripartita*	4[f]	15	Operon, UBC
Artemisia cana ssp. *cana* × *A. tridentata* ssp. *wyomingensis*	3[g]	6	Operon, UBC

[a] Operon = Operon Technologies, Inc., UBC = University of British Columbia Biotechnology Laboratory.

[b] OPH-12, OPAF-06, OPAP-01, OPAP-03, APOR-03, APAW-04, UBC-208, UBC-275, UBC-285, UBC-302, UBC-345, UBC-356, UBC-358, UBC-361, UBC-409, UBC-413, UBC-421, UBC-425, UBC-456, UBC-769, UBC-770, UBC-772

[c] OPAP-01, OPAP-07, OPAW-04, UBC-208, UBC-270, UBC-285, UBC-302, UBC-341, UBC-356, UBC-358, UBC-361, UBC-413, UBC-421, UBC-534, UBC-536, UBC-542, UBC-571, UBC-584, UBC-585, UBC-595, UBC-598, UBC-769, UBC-770, UBC-772

[d] See Table 3.

[e] OPF-19, OPJ-04, OPU-03, OPU-17, OPW-07, OPW-08, OPW-17, OPX-12, OPY-01, OPY-02, OPY-10

[f] UBC-208, UBC-285, UBC-358, UBC-425

[g] OPAP-01, UBC-241, UBC-245

TABLE 3. Primer name, sequence, and number of markers generated from each primer used for amplification of sample DNA for study 2 (2*x* and 4*x* *Artemisia tridentata* ssp. *vaseyana* populations.

Primer name[a]	Primer sequence (5′→3′)	Number of markers
UBC-157	CGTGGGCAGG	11
UBC-180	GGGCCACGCT	12
UBC-199	GCTCCCCCAC	12
UBC-457	CGACGCCCTG	5
UBC-459	GCGTCGAGGG	8
UBC-515	GGGGGCCTCA	10
UBC-540	CGGACCGCGT	9
UBC-542	CCCATGGCCC	9
UBC-563	CGCCGCTCCT	7
UBC-584	GCGGGCAGGA	16
UBC-592	GGGCGAGTCC	5
UBC-598	ACGGGCGCTC	10
UBC-601	CCGCCCACTG	10
UBC-615	CGTCGAGCGG	9

[a] University of British Columbia Biotechnology Laboratory, Vancouver, BC

4*x* with the exception of 5 Hobble Creek and 1 Kolob Terrace 2*x* plants.

STUDY 3.—DNA marker similarities among the putative hybrid plants and their parents are illustrated in Figure 6. The 1st hybrid combination (*A. tridentata* ssp. *tridentata* × *A. t.* ssp. *vaseyana*), which had been confirmed by previous studies (McArthur et al. 1988, Weber et al. 1994, Messina et al. 1996), yielded 3 major groups plus several outliers (Fig. 6). The major groups are the *A. tridentata* ssp. *vaseyana* parent (top), the F_1 and F_2 hybrids (center), and the *A. t.* ssp. *tridentata* parent (near bottom). The outliers are some *A. t.* ssp. *tridentata* parent plants and especially F_2 plants (near bottom of top group and near bottom). These results of a parent through F_2 hybrid generations give evidence of hybridization. The parent plants are well separated in the phenogram (Fig. 6). The F_1 and F_2 plants are closer to the maternal parent than expected. F_2 hybrids do, however, show additional segregation over the F_1 plants as expected (Fig. 6). Similarity values of Figure 6 are less than others presented herein and in McArthur et al. (1998) because we worked with taxon-specific markers to the extent that we could find them; therefore the values should be considered relative and not absolute. The other 2 putative hybrid combinations (*A. tridenata* ssp. *wyomingensis* × *A. tripartita* and *A. cana* ssp. *cana* × *A. tridentata* ssp. *wyomingensis*) gave contrasting results (data not shown). The *A. tridentata* ssp. *wyomingensis* × *A. tripartita* combination was not successful. All female parent plants ($N = 10$), progeny of self-pollinated control plants ($N = 7$), and putative hybrid plants ($N = 15$) clustered in 1 stem above 50% similarity, whereas pollen parents (2 different *A. tripartita* populations, each $N = 6$) clustered in a separate group above 40% similarity. The 2 groups are only about 22%

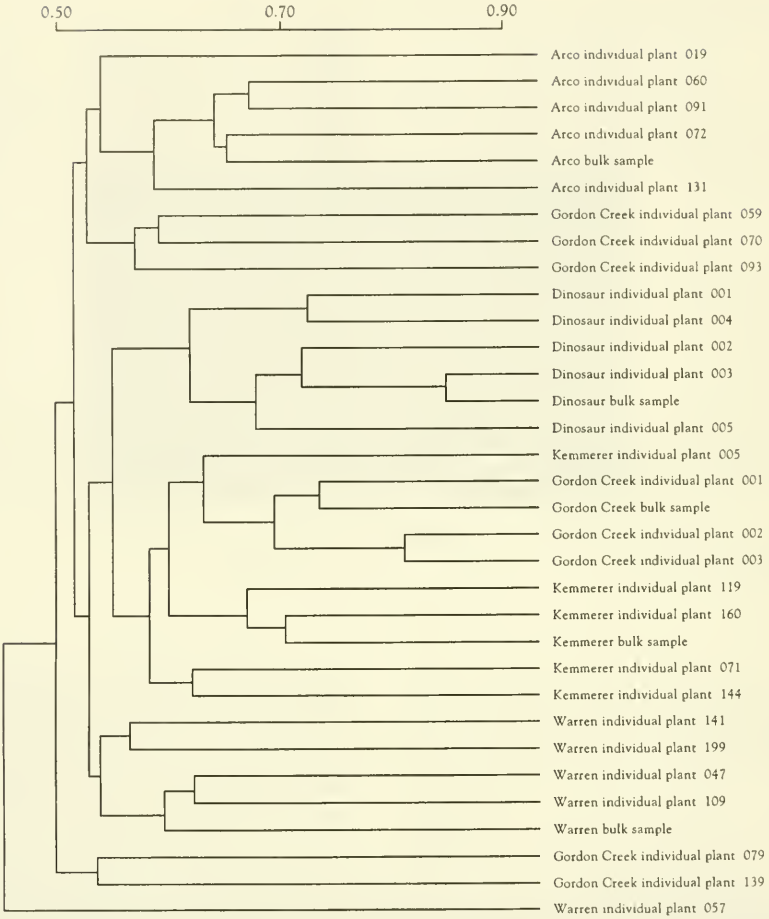


Fig. 3. Phenogram produced using UPGMA clustering analysis (NTSYS-pc, Rohlf 1993) for 5 *Artemisia tridentata* ssp. *wyomingensis* populations. Individual plants and bulked samples are included.

similar. The *A. cana* ssp. *cana* × *A. tridentata* ssp. *wyomingensis* combination, on the other hand, yielded results that had several putative hybrid plants intermediate in similarity to the 2 parental stocks. These results are corroborated, in part, by cytological studies. The *A. cana* ssp. *cana* × *A. tridentata* ssp. *wyomingensis* combination yielded 6*x* plants, which would be expected in an 8*x* (*A. cana* ssp. *cana*) × 4*x* (*A. tridentata* ssp. *wyomingensis*) combination. Because both *A. tridentata* ssp. *wyomingensis* and *A. tripartita* are 4*x*, cytological results are not instructive in that combination. Meiotic figures of this combination display numerous multivalents, especially quadrivalents, as did *A. tridentata* ssp. *wyomingensis* plants and other polyploid taxa in an earlier cytological study (McArthur et al. 1981).

DISCUSSION

USE OF RAPD MARKERS.—The set of studies reported herein adds weight to the evidence that RAPD markers are useful in systematic problems at various hierarchical levels from individual plants to genera (e.g., Levi et al. 1993, Santos et al. 1994, Van Buren et al. 1994, Gang and Weber 1995, McArthur et al. 1998) and in hybridization problems including hybrid zones and natural and artificial hybridizations (e.g., Huen and Helentjaris 1993, Bradshaw et al. 1994, Kennard et al. 1994, Dean and Arnold 1996, Lin and Ritland 1996, Mudge et al. 1996).

GENETIC DIFFERENTIATION AT VARIOUS SYSTEMATIC LEVELS.—The amount of genetic differentiation among individual plants within

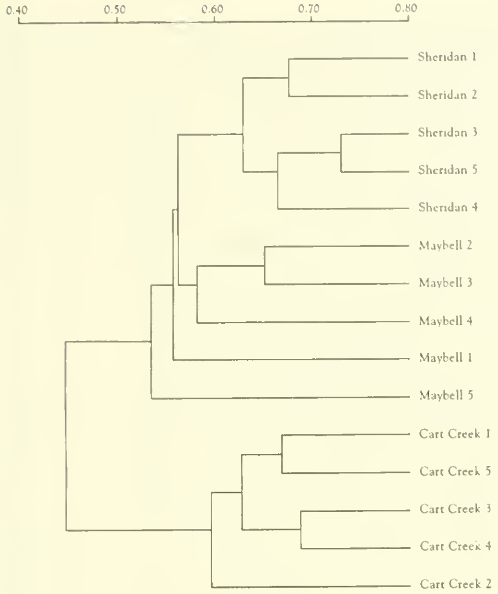


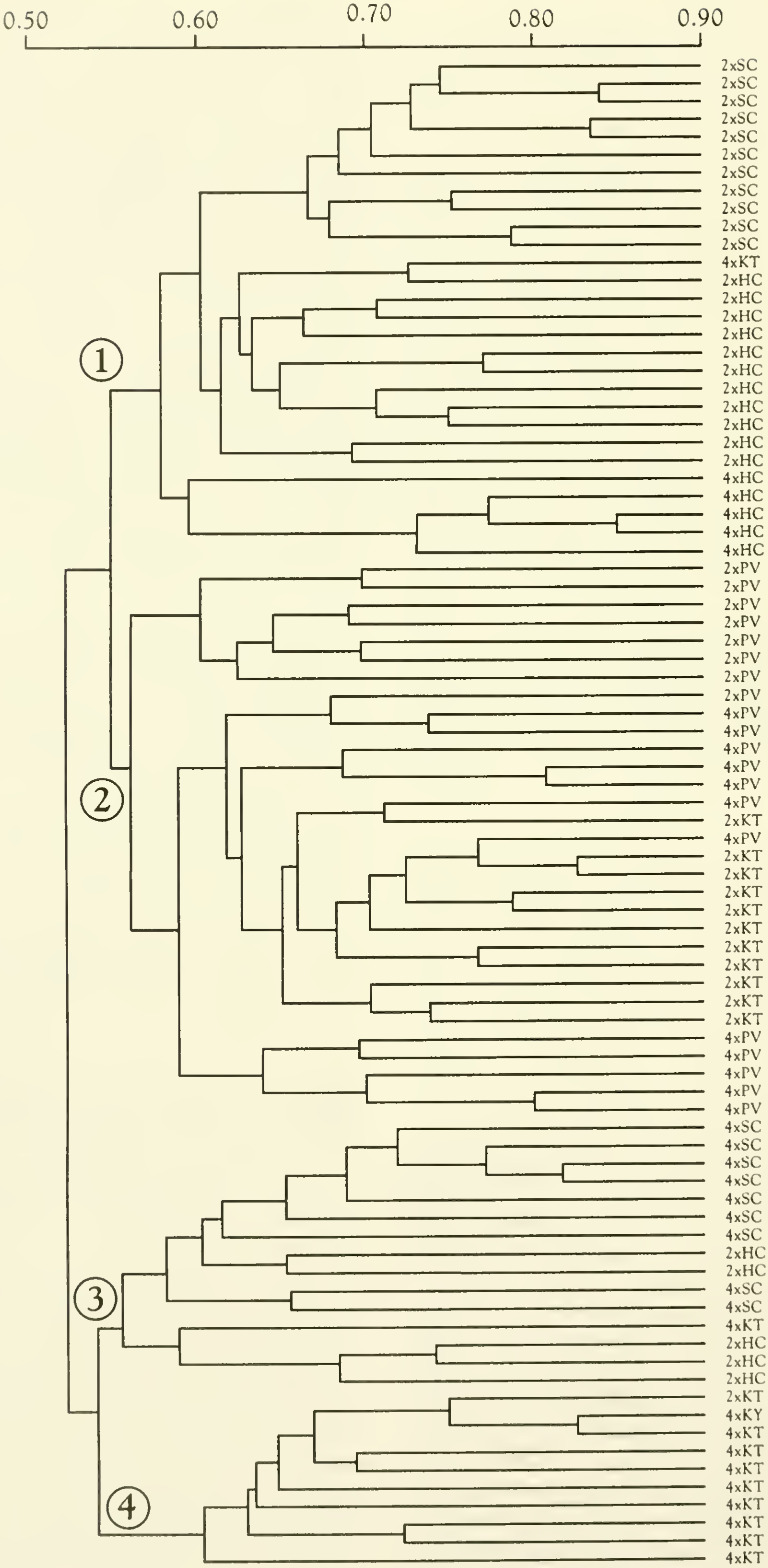
Fig. 4. Phenogram produced using UPGMA clustering analysis (NTSYS-pc, Rohlf 1993) for *Artemisia cana* subspecies and populations. Individual plants are as follows: *A. cana* ssp. *cana*, Sheridan (individual plants 1–5), Maybell (individual plants 1–5); *A. cana* ssp. *viscidula*, Cart Creek (individual plants 1–5).

populations as revealed by genomic DNA markers in this set of studies (Figs. 3–6) is similar to that of populations determined by bulked samples (Fig. 3; Van Buren et al. 1994, Gang and Weber 1995, McArthur et al. in review). Similarity between individual plants within populations is usually in the range of 50–85%. An exception is in the *A. tridentata* ssp. *tridentata* × *A. t.* ssp. *vaseyana* hybridization study (Fig. 6), where fewer subspecies contrasting markers were used and similarity in hybrid and parental plants ranges from 20% to 100% Most plants within populations of that study are above 50% in similarity, but several outliers are only about 20–25% similar to other plants in their populations.

We suspect that individual plants are as different from one another within closely spaced populations as populations within taxa are from one another because of the wind-pollinated nature of the *Tridentatae* (McArthur et al. 1979, 1988, McArthur 1989). In a wind-pollination system, pollen of landscape-dominant plants is dispersed not only within populations but also between populations (Grant 1975, Franklin 1981, McArthur 1989). Further evidence of the spread of *Tridentatae* pollen is that during its fall pollination season, *Tridentatae* (= sagebrush) pollen counts are given out by weather reporters to the public in areas removed from stands of plants for the benefit of those allergic to *Tridentatae* pollen.

Subspecies range from 25% (*A. tridentata*; see Fig. 6) to 45% (*A. cana*; see Fig. 4) similarity among populations, which is generally more similar than the between-species similarities reported in the genera *Ranunculus*, *Artemisia*, and *Sphaeromeria* except for closely related (usually within same subgenus) species (Van Buren et al. 1994, McArthur et al. 1998). The 25% value may be low because DNA markers were selected to contrast the subspecies. Between-genera similarity values in a companion study (McArthur et al. 1998) were also lower, 7–18%.

DE NOVO ORIGIN OF 4*x* *A. TRIDENTATA* SSP. *VASEYANA*.—Cytological evidence (karyotypic structure and high multivalent frequencies in polyploids) suggests that the *Tridentatae* include a high frequencey of autopolyploidy (McArthur et al. 1981). DNA marker data (Fig. 5) are useful in addressing the hypothesis that 4*x* populations and plants that are adjacent or intermixed with 2*x* populations may be of *de novo, in situ* origin. Data suggest that the hypothesis is at least partially correct. The 4*x* plants from near Pine Valley fall within the same grouping as the nearby 2*x* plants from Pine Valley and Kolob Terrace (Fig. 5). We suggest that these 4*x* plants are of *de novo* origin from the local 2*x* population(s). Cytological evidence gives additional credence to this hypothesis as we have located 3 populations in the Pine Valley area that are indistinguishable morphologically and chemically (coumarin compound content) but contain individual 2*x* and 4*x* plants (McArthur and Sanderson in review). Since the other 4*x* populations (Salina Canyon and Kolob Terrace) did not cluster tightly with adjacent 2*x* populations, they may not be recent autoploids. However, our studies show that all sampled *A. tridentata* ssp. *vaseyana* plants are quite similar (above 50%; see Fig. 5), suggesting earlier or more distant autopolyploidy as the source of 4*x* populations. These 4*x* populations have apparently dispersed, given the evident intertwining DNA marker (Fig. 5) and geographic patterns (Fig. 1). Recently,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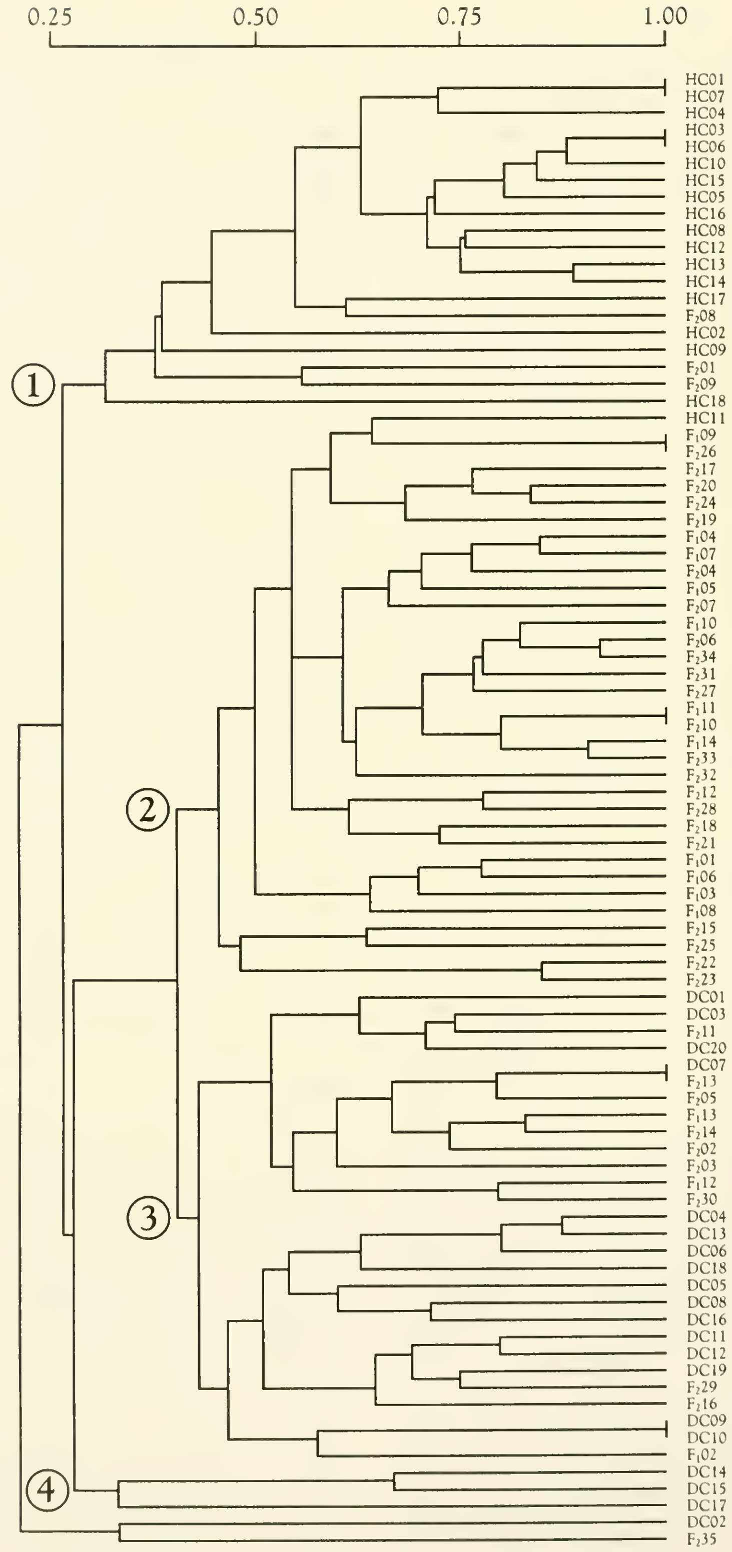
autopolyploidy has been recognized as playing a more important role in evolution in a wide array of plant species than has been traditionally recognized, e.g., Small 1985, Bayer 1987, Ness et al. 1989, Lumaret et al. 1989, Van Dijk et al. 1992, Soltis and Soltis 1993, Bretagnolle and Thompson 1996, Laushman et al. 1996. We believe the data we present here give further credence to the importance of autopolyploidy in *Tridentatae*.

RAPD CONTRIBUTION TO HYBRIDIZATION STUDIES IN *TRIDENTATAE*.—The *Tridentatae* are thought to have evolved through a pattern of geographic migration, introgression, and hybridization (Ward 1953, Beetle 1960, Hanks et al. 1973, McArthur and Plummer 1978, McArthur et al. 1981, 1988, Thompson 1991). Therefore, studies that contribute to the understanding of hybridization processes in the group are needed to better understand the group's dynamic population biology and evolution. Our DNA marker data are from 3 different hybrid combinations. These data confirm the hybrid nature of the *A. tridentata* ssp. *tridentata* × *A. t.* ssp. *vaseyana* progeny previously studied by other techniques (McArthur et al. 1988, 1992, Weber et al. 1994, Messina et al. 1996). The segregation of RAPD markers in F_1 and F_2 generations is a pattern that can be explained as the consequence of hybrid segregation (Fig. 6). Our data also support a successful hybridization of the *A. cana* ssp. *cana* × *A. tridentata* ssp. *wyomingensis* combination. Seven of the 13 putative hybrid plants examined for RAPD markers are intermediate in marker patterns in respect to their parents, whereas 6 are similar to the maternal parent. These results are consistent with our previous results on hybridization wherein substantive fractions of the progeny of successful hybrid combinations are indeed of hybrid origin and other substantive fractions are the result of self-pollinations (McArthur et al. 1988). The other hybrid combination, *A. tridentata* ssp. *wyomingensis* × *A. tripartita*, was not successful. All putative hybrid progeny are similar to their maternal parents.

These hybrid combinations, aside from helping us better understand *Tridentatae* breeding systems, were made for specific purposes (McArthur et al. 1985, 1988, 1992, McArthur 1988). The *A. tridentata* ssp. *tridentata* × *A. t.* ssp. *vaseyana* combination has been extended to the F_4 generation with the goal of maintaining the growth and woody biomass characteristics of the paternal parent and the leafiness and palatability (= essential oil profile) to large ungulates of the maternal parent. We are currently evaluating those characteristics as well as the adaptation of the hybrids with respect to parental stock (Noller and McArthur 1986, McArthur et al. 1988, Weber et al. 1994, Messina et al. 1996, McArthur unpublished). The other 2 hybrids were made to combine the drought tolerance and widespread adaptability of the landscape-dominant *A. tridentata* ssp. *wyomingenis* with the root-sprouting, fire-tolerance capabilities of *A. cana* ssp. *cana* or *A. tripartita* (Beetle 1960, McArthur 1994). Much of the natural range of *A. tridentata* ssp. *wyomingensis* has been lost to cheatgrass and other alien fire-tolerant annual weeds (McArthur et al. 1990, Monsen and Kitchen 1994). The successful F_1 hybrids have been outplanted and are apparently fertile (we recently collected filled seed). Additional evaluation of both successful hybrid lines is necessary before they can be considered for wide-scale planting. Morever, the use of such material should be critically evaluated by land managers and others with interest in the well-being of our landscapes.

We have discussed some traits in *Tridentatae* species and hybrids that might be desirable to combine. The location of such traits on a genetic map would be useful information. RAPD, in concert with other molecular genetic tools and additional hybrid stock, could be used to document chromosomal locations as has been done with other plants, e.g., Penner et al. 1993, Bradshaw et al. 1994, Kennard et al. 1994, Santos et al. 1994, 1995, Mudge et al. 1996. Such information would also be useful in the ongoing work of understanding the dynamics of hybrid zones between the subspecies of *A. tridentata* (McArthur et al. 1988, Freeman et al. 1991, 1995, Weber et al. 1994, Graham et al. 1995, Messina et al. 1996, Wang et al. 1997).

Fig. 5 (see facing page). Phenogram produced using UPGMA clustering analysis (NTSYS-pc, Rohlf 1993) for *Artemisia tridentata* ssp. *vaseyana* 2*x* and 4*x* populations. Individual plants are keyed as follows: 2*x* = diploid, 4*x* = tetraploid, HC = Hobble Creek, KT = Kolob Terrace, PV = Pine Valley, SC = Salina Canyon. See Figure 1 and Table 1 for more detailed location information. Circled numbers, e.g., ①, are the major groups discussed in the text.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$F_2$35

Fig. 6 (see facing page). Phenogram produced using UPGMA clustering analysis (NTSYS-pc, Rohlf 1993) for *Artemisia tridentata* ssp. *tridentata* × *A. t.* ssp. *vaseyana* including parental and F_1 and F_2 plant populations. Individual plants are keyed as follows: DC = *A. t.* ssp. *tridentata* parent plant (Dove Creek), HC = *A. t.* ssp. *vaseyana* parent plant (Hobble Creek), F_1 = 1st generation hybrid plant, F_2 = 2nd generation hybrid plant. Circled numbers, e.g. ①, are the major groups discussed in the text.

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BITTERBRUSH (*PURSHIA TRIDENTATA* PURSH) GROWTH IN RELATION TO BROWSING

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ABSTRACT.—The objectives of this study were to compare vegetative and reproductive growth characters of bitterbrush (*Purshia tridentata* Pursh) stands as they relate to browsing levels. Growth characters were measured on 10 ecologically diverse stands in southwestern Montana on which browsing ranged from 0% to 60% of all current annual long shoot (LS) growth. Bitterbrush plants exhibited both twig-level and plant-level responses to browsing. Total bud density per plant was similar for browsed and unbrowsed sites, but differed ($P < 0.01$) between browsed and unbrowsed twigs. Browsed twigs produced one-half the leaf cluster density produced by unbrowsed twigs. No significant ($P < 0.05$) relationship between browsing levels on browsed plants and bud densities was found. Length of old-growth twigs per plant was shorter ($P < 0.001$) on browsed sites than on unbrowsed sites. Burning at 2 environmentally paired sites reduced flower bud density ($P < 0.001$) 9 and 10 growing seasons later although LS length was not affected. Growth of LS showed a site-by-year interaction ($P < 0.05$). Our data suggest that long-term unbrowsed plants should not be used as a standard for comparison with normally browsed plants.

Key words: Purshia tridentata, *bitterbrush, browsing, shoot growth, bud development, Montana.*

Antelope bitterbrush (*Purshia tridentata* Pursh), well documented as a valuable food source for big-game animals (Kufeld 1973, Kufeld et al. 1973), is highly palatable, moderately nutritious, and common on many big-game winter ranges (Giunta et al. 1978), although it seems to be declining in some areas (Winward and Findley 1983). Bitterbrush is found in a wide range of habitats (Franklin and Dyrness 1973) and is useful as a ground stabilizer on exposed soils (Nord 1959). Therefore, land managers are interested in its propagation, growth, and management to improve degraded wildlife habitat.

Known for its variability in habitat, morphology, and physiology, bitterbrush ranges from prostrate forms only 10 cm high to columnar forms over 3 m tall (Winward and Findley 1983). Color, shape, and size of leaves, stems, and seeds vary between and within populations (Alderfer 1977). Mowing and burning result in responses that range from death to vigorous sprouting (Clark et al. 1982). While these adaptations enable bitterbrush to inhabit widely divergent habitats in western North America, they can also make management of the species more difficult unless the response of local populations is known.

Guenther (1989) studied the environmental relationships of bitterbrush stands on Montana Fish, Wildlife, and Parks' Mount Haggin Wildlife Management Area (MHWMA) in southwestern Montana and noted the wide range of habitats and stand growth. Guenther (1989) also found a high level of browsing on bitterbrush plants and little successful reproduction during the previous decade. Wambolt et al. (1996) compared some of the same MHWMA sites with 5 other southwestern Montana locations and found differences in crude protein content by site.

The specific objectives of this study were to compare vegetative and reproductive growth characters of 10 bitterbrush stands on and near the MHWMA and to relate them to browsing levels. We hypothesized that plants from nearby bitterbrush stands are not uniform in their growth characteristics.

METHODS

Study Sites

We chose 10 study sites primarily to represent bitterbrush stands from a range of environmental conditions (Table 1). Included were a burned site and sites protected from browsing.

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All sites are located within a radius of 14.5 km near Butte and Anaconda in southwestern Montana. Long-term climatic records were available for the general study area from the Anaconda weather station at 1700 m elevation. Annual precipitation at Anaconda averages 340 mm, with 47% received between April and July (NOAA 1991).

Vegetation types at all but 3 sites (Burn, Unburn, and High Rye) are seral stages of the bitterbrush–bluebunch wheatgrass (*Agropyron spicatum* Pursh) habitat type (Mueggler and Stewart 1980). The dominant shrub is bitterbrush, but understory vegetation is regressed primarily from grazing (Fraas et al. 1992) on the other 7 sites from the described potential climax composition (Youtie et al. 1988).

We selected the Butte site at Maude S Canyon, near Butte, Montana, because it receives no ungulate browsing. The plant community consists of bitterbrush, *Centaurea maculosa* Lam. (spotted knapweed), *Ribes cereum* Dougl. (squaw currant), and *Rosa woodsii* Lindl. (Woods rose).

At Dry Cottonwood Creek in the Deerlodge district of the Deerlodge National Forest, we studied a 2-part exclosure. One portion, known as the Deer exclosure, was game proof. The other half allowed deer use but served as a livestock exclosure and thus was known as the Cattle exclosure. Near the exclosure, we studied a bitterbrush stand known as the Cattle + Deer site because it sustained both cattle and mule deer browsing. These 3 sites have a scattered overstory of *Pseudotsuga menziesii* [Mirb.] Franco (Douglas-fir). A large number of native perennial forbs occur in the understory on these sites.

To gauge the impacts of burning bitterbrush in southwestern Montana, we selected 2 sites. These sites (Burn, Unburn) were environmentally paired on both sides of a burn line on the south flank of Steep Mountain, 8 km northwest of Butte, in the Butte district of the Deerlodge National Forest. The plant community on these 2 sites is a bitterbrush–mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle)–bluebunch wheatgrass association intermediate to the big sagebrush–bluebunch wheatgrass and bitterbrush–bluebunch wheatgrass habitat types of Mueggler and Stewart (1980). The prescribed burn was conducted 3 November 1981 after a year's rest from livestock grazing on both sites to increase fuel loads. Livestock use on both sites resumed 15 September 1982.

TABLE 1. Topographic characteristics of the 10 study sites. Data from the last 4 sites were obtained from Guenther (1989).

Site	Elevation (m)	Slope (%)	Aspect (°)
Butte	1730	26	234
Deer exclosure	1830	12	225
Cattle exclosure	1830	16	188
Cattle + Deer	1820	10	190
Burn	2010	22	200
Unburn	2010	22	200
Powerline	1640	16	85
Willow Creek	1780	31	110
Railroad Gulch	1650	32	115
High Rye	1940	38	120

Four sites were located on the MHWMA, owned and managed by Montana Fish, Wildlife, and Parks. The Powerline site is on a slope 50 m above a perennial stream on the northeast edge of the MHWMA big-game winter range. The plant community consists of bitterbrush and spotted knapweed. The Willow Creek site, near the top of a grassy ridge 150 m above Willow Creek, supports a relatively large amount of *Elymus cinereus* Scribn. & Merr. (basin wild rye), along with other perennial grasses and bitterbrush. This area was used as winter range by mule deer, elk, and moose. The Railroad Gulch site is also on the deer and elk winter range. This site occupies a midslope position 30 m above an intermittent stream, where the plant community consists of bitterbrush and spotted knapweed. The High Rye site, 1500 m higher in elevation than the other MHWMA sites, appears to receive the greatest snowpack. The plant community on the High Rye site is typical of the bitterbrush–rough fescue (*Festuca scabrella* Torrey ex Hook.) habitat type (Mueggler and Stewart 1980), with those species currently dominant. Guenther (1989) found the least amount of big-game use at this location among the 4 MHWMA sites. The MHWMA study sites received insignificant levels of livestock grazing.

Sampling and Analyses

Study sites typical of their communities were delineated by five 15-m transect lines placed perpendicular to the slope at 3-m intervals, thus comprising a study plot of 15 × 12 m. We recorded topographic information at each site, determining aspect by taking a compass bearing from the major slope, measuring slope with a clinometer, and ascertaining elevation from USGS topographic maps. The information from MHWMA sites was taken from Guenther (1989).

We used the following definitions during the study: **bitterbrush plant**—a single stem or group of stems with a single point of origin; **leaf cluster**—a bud which had produced a group of leaves and which had not elongated (<7 mm in length); **long shoot (LS)**—a bud structure that had elongated (>7 mm in length) in the current growing season and consisted of a stem and attached leaf clusters; **flower**—a bud which had produced a flower; flowers grew only on 1-yr-old or older stems.

Two bitterbrush plants rooted within 1 m of each transect line were randomly selected for measurements (10 plants per site). We randomly chose 4 branches on each plant using a frame with 10-cm grids placed on top of the plant. Random numbers identified grid intersections. The closest live branch to a plumb line dropped through the grid was sampled. On each sampled branch we recorded the following: age and length of each stem segment, length of LS, number of flowers, leaf clusters, and LS. Apical bud status of each terminal LS segment was recorded as browsed (within the past year), unbrowsed, or dead. Flowers were counted in early July, and leaf clusters and LS were counted and measured in early September. We compared measurements only from branch (LS) segments ≤3 yr old, as little bud activity occurred on older portions of the branches. To determine age, we examined annual growth scars after an initial trial of comparing growth scars with growth rings. These measurements were summarized across all 4 branches sampled per plant to create a plant average for each category. Overall averages resulted from averaging the 10 plant averages for each of the 10 study sites (100 plants).

We observed each sampled branch for browsing use during the previous winter. Guenther (1989) found a high correlation ($r = 0.94$, $P < 0.0001$) in measuring percent bitterbrush utilization by determining either percentage of LS browsed or length of LS removed; thus, we determined the percentage of total LS browsed. All branches were considered, regardless of availability to browsers, to determine plant response to removal of a percentage of total annual growth to relate to previously recommended use levels (Hormay 1943, Garrison 1953, Martinsen 1960, Lay 1965, Urness and Jensen 1983). Browsing-level analyses were conducted by comparing the number of browsed and unbrowsed live LS on each plant in the manner detailed by Wambolt (1996). Browsed and unbrowsed twigs on a plant were each pooled across branches for comparison of browsing response on a plant level. By combining plant averages we then created averages for the 10 sites.

Occurrence of unequal variances for comparisons, as experienced by Bilbrough (1990) with similar data, required use of nonparametric statistical tests (Sokal and Rohlf 1981): a Wilcoxon signed-rank test (Snedecor and Cochran 1989) for comparison of paired measures (such as the same plants between years), and a Mann-Whitney rank-sum test (Snedecor and Cochran 1989) for comparison of group means, both at $P < 0.05$. Interactions between years, sites, and treatments were analyzed with a multi-factor analysis of variance (Snedecor and Cochran 1989). Correlation was used to measure the relationship between some variables without a dependence relationship (Snedecor and Cochran 1989). Comparisons between sites were based on least significant difference (LSD; Snedecor and Cochran 1989) at $P < 0.05$. Least significant differences were calculated as part of the analysis of variance for pairs of means, such as site-to-site or year-to-year comparisons. All statistical tests were programs of the MSUSTAT statistical program (Lund 1991).

RESULTS AND DISCUSSION

Browsing Effects

At the 8 browsed sites the browsing level ranged from 23% to 60% removal of all current annual LS (Table 2). This range was within previously recommended levels for long-term health and maintenance of stands (Hormay 1943, Garrison 1953, Steinhoff 1959, Martinsen 1960, Lay 1965, Shepherd 1971). Only 2 sites had less browsing the 2nd winter ($P < 0.05$), while the other 6 were browsed at nearly the same level both years. During 1990 the 8 sites were equally browsed, but in 1991 some variation in browsing levels occurred

TABLE 2. Browsing level (percent) for 1990 and 1991 at the study sites, based on number of total long shoots (LS) removed.

Site	1990	1991
Butte	0^{a}[1]^{x}[2]	0^{az}
Deer exclosure	0^{ax}	0^{az}
Cattle exclosure	45^{aw}	39^{awxy}
Cattle + Deer	55^{aw}	54^{axy}
Burn	48^{aw}	50^{axy}
Unburn	51^{aw}	61^{ay}
Powerline	51^{aw}	40^{awxy}
Willow Creek	52^{aw}	23^{bw}
Railroad Gulch	53^{aw}	37^{awxy}
High Rye	60^{aw}	30^{bwx}

[1] Row entries with similar lowercase letters (ab) are not significantly different (Wilcoxon test, $P < 0.05$).

[2] Column entries with similar lowercase letters (wxyz) are not significantly different (LSD, $P < 0.05$).

among sites. Evaluation of browsing effects should consider that post-browsing LS length represents the sum of each year's growth minus the cumulative reduction by browsing. In addition to the direct effect of removing twig material, browsing might also affect length by changing the potential for growth. Growth potential might be affected by the ability of the whole plant to grow or by the number or type of buds available, either for the whole plant or for individual twigs.

Total bud density per plant, expressed as the sum of the number of flowers, leaf clusters, and LS per unit length of stem, was similar for browsed and unbrowsed sites ($P > 0.10$; Fig. 1). However, total bud density did differ at the twig level ($P < 0.01$) between browsed and unbrowsed twigs (Fig. 1). Browsed plants had a lower flower bud density ($P < 0.001$) and higher LS bud density ($P < 0.01$) than unbrowsed plants (Fig.1). However, at the twig level (Fig. 1), flower or LS densities were similar between browsed and unbrowsed twigs pooled for all browsed sites. Unbrowsed twigs from browsed plants had lower flower ($P < 0.01$) and higher LS ($P < 0.001$) bud densities than twigs from unbrowsed plants. This suggests that browsing affects both browsed and unbrowsed twigs on browsed plants, which is a plant-level response. Further, density of any of the 3 types of buds did not appear to depend on actual level of browsing per plant, as 0% to 100% of terminal twigs were browsed on sampled branches on plants exposed to herbivores, with $r = 0.07$ ($P > 0.22$) between bud density and percentage browsed. This suggests that any degree of browsing affects flower and LS production on the whole branch and probably on the whole plant.

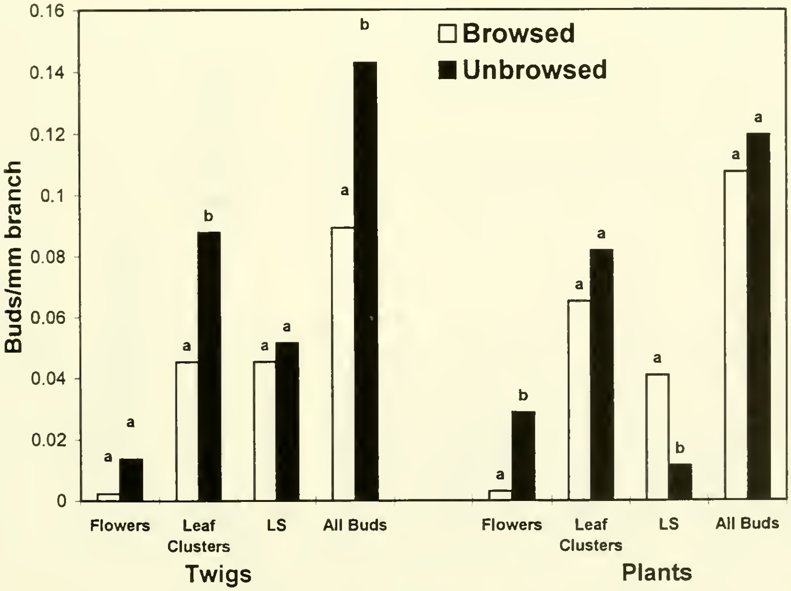

Fig. 1. Average number of buds per mm of branch (density) by type of bud structure (flowers, leaves, long shoots). Comparisons are between browsed and unbrowsed twigs on browsed plants ($n = 8$), and between plant averages from browsed ($n = 7$) and unbrowsed ($n = 2$) sites. Pairs of bars with similar letters are not different (Mann-Whitney test, $P < 0.05$).

Several researchers have attributed low growth rates to whole-plant effects on vigor (Hormay 1943, Garrison 1953) or carbohydrate reserves (Menke and Trlica 1983) and have recommended moderate browse levels or specific seasons of use. Tueller and Tower (1979) reported a lower growth rate in rested or lightly used plants than in those that were heavily browsed, terming this a stagnation effect. Bilbrough (1990) found that clipped bitterbrush was able to mobilize inactive buds for elongation and hypothesized that this would eventually alter flower and LS ratios. Although we could detect differences in bud density (buds per unit length of stem) between sites and treatments and could construct bud frequencies from this information, we could not determine whether changes in frequency of flowers, leaf clusters, or LS were due to variable densities before browsing or to bud differentiation after browsing.

Leaf cluster bud density was 49% lower on browsed twigs ($P < 0.05$) than on unbrowsed twigs (Fig. 1). This decrease did not appear between browsed and unbrowsed plants or between unbrowsed twigs from browsed plants and twigs from unbrowsed plants, suggesting that this leaf bud response occurred only on browsed twigs. Possible mechanisms for this decline include increased mortality of leaf buds either by physiological effects or by higher leaf bud density at the distal (browsed) end of the twig. Physiological effects could include physical or chemical damage due to browsing or a change in resource allocation patterns within the plant to maintain flower and LS bud numbers at the expense of leaf bud numbers.

Although browsing levels (Table 2) were statistically the same for the Burned and Unburned sites, flower bud density was lower on the Burned site (Table 3) than on the Unburned site ($P < 0.001$). Leaf cluster and LS densities were similar between the two sites ($P > 0.10$), apparently unaffected 9 and 10 growing seasons after the fire. Fraas et al. (1992) had earlier reported that bitterbrush on the Burned site was significantly lower in canopy cover ($P > 0.01$), flower production ($P > 0.1$), and seed production ($P > 0.1$) than on the Unburned site. Because these 2 sites were adjacent and environmentally the same (Table 1), including their management before and after the burn treatment, it is logical to assume that flower bud density was lowered by the fire just as were the characteristics reported by Fraas et al. (1992). We could not find additional burned sites to include in our investigation. Therefore, we are uncertain whether similar results would be the rule, but our findings indicate that a reduction in flower buds should be anticipated.

The Dry Cottonwood Cattle exclosure site had lower total bud densities than the unbrowsed Deer exclosure site ($P < 0.01$), whereas flower bud densities (Table 3) were lower ($P < 0.001$) and LS bud densities were higher ($P < 0.001$) in 1990, as were most other browsed to unbrowsed comparisons. Although browse levels (Table 2) were not significantly different ($P < 0.10$) between the Dry Cottonwood Cattle exclosure and Cattle + Deer sites, in 1990 the Cattle + Deer site had twice as many LS buds per unit length of stem (Table 3). Other bud densities did not differ ($P < 0.05$) between

TABLE 3. Bud density (buds per 100 mm stem) for flowers, leaf clusters, and long shoots (LS) on all study sites in 1990 and 1991. The 2 unbrowsed study sites are at left.

Bud type	Year	Butte	Deer excl	Cattle excl	Cattle + Deer	Burn	Unburn	Power Line	Willow Creek	RR Gulch	High Rye
Flower	1990	7.5^{f1y1}	6.9^{cfy}	0.4^{ay}	0.7^{aby}	0.1^{ay}	2.9^{bcdy}	1.6^{abcy}	3.5^{cdy}	2.2^{abcy}	5.0^{dey}
	1991	2.7^{cz}	2.5^{cz}	0.0^{ay}	0.7^{aby}	0.1^{aby}	1.1^{bz}	0.1^{aby}	0.3^{abz}	0.4^{abz}	0.1^{abz}
Leaves	1990	10.7^{cy}	7.3^{ay}	8.1^{abcy}	7.9^{aby}	10.3^{bcy}	9.7^{abcy}	8.9^{abcy}	9.5^{abcy}	10.0^{bcy}	10.5^{bcy}
	1991	6.3^{abcz}	8.9^{cy}	6.7^{abcy}	5.6^{abz}	4.1^{az}	6.2^{abcz}	8.2^{bcy}	3.5^{az}	8.6^{bcy}	4.5^{az}
LS	1990	1.7^{aby}	1.1^{ay}	3.2^{cdy}	6.1^{cy}	4.6^{dy}	3.2^{cdy}	3.4^{cdy}	3.1^{bcy}	2.1^{abcy}	3.0^{bcy}
	1991	1.0^{ay}	1.0^{ay}	2.4^{aby}	3.5^{bcdz}	2.3^{abz}	2.6^{abcy}	4.7^{dcy}	3.7^{cdy}	3.3^{bcz}	6.0^{cz}

[1] Row entries with similar letters (abcdef) are not significantly different (LSD, $P > 0.05$).

[2] Site entries with similar letters (yz) for year pairs are not significantly different (Wilcoxon test, $P > 0.05$).

the 2 sites. Few differences for any type of buds were found among browsed unburned sites or between the 2 unbrowsed sites (Table 3).

Growth

We measured old-growth branch length (3-, 2-, and 1-yr-old segments), LS growth (annual growth), and leaf weights (leaf clusters). Total branch length of old-growth twigs per plant (Fig. 2) was considerably shorter on the 8 browsed sites than on the unbrowsed Butte and Deer exclosure sites ($P < 0.001$), reflecting the influence of browsing in modifying branch length. Accordingly, at the Dry Cottonwood location the unbrowsed site had longer branches than the Cattle exclosure site ($P < 0.01$; with only deer browsing), whereas the Cattle + Deer site had the shortest branches ($P < 0.05$). Total branch length per plant (Fig. 2) at the Burned and Unburned Steep Mountain sites did not differ ($P < 0.10$), which indicates that the combination of growth and browsing (Table 2) was similar between these sites for the previous 3 yr.

The number and length of LS produced varied by site and year, with 3 sites having fewer LS (Fig. 3) and 3 sites having longer ($P < 0.05$) LS in 1991 than in 1990 (Fig. 4). However, because these differences were not always at the same sites, the correlation between number and average LS length was not significant ($r = -.12$, $P > 0.60$). As discussed earlier (Fig. 1), LS bud density was highest on browsed plants ($P < 0.01$). However, LS bud numbers (Fig. 3) generally did not differ ($P < 0.10$) between browsed and unbrowsed plants largely because of longer branches on unbrowsed plants (Fig. 2).

Total LS length (annual growth; Fig. 5) was not significantly correlated to total branch length ($r = 0.45$, $P > 0.13$) across all sites. Although the unbrowsed Butte and Deer exclosure sites that had the longest branches also had high total LS growth, this total length was not significantly ($P < 0.10$) longer than on most browsed sites (Fig. 5).

Long shoot length per unit length of branch varied between several sites and sometimes between years (Fig. 6). This growth rate generally increased on the MHWMA sites (Powerline, Willow Creek, Railroad Gulch, and High Rye) in 1991, although all other sites decreased. Neither total LS length (Fig. 5) nor LS length per unit of branch (Fig. 6) differed between the Burned and Unburned sites, although the Unburned site had significantly ($P < 0.01$) more

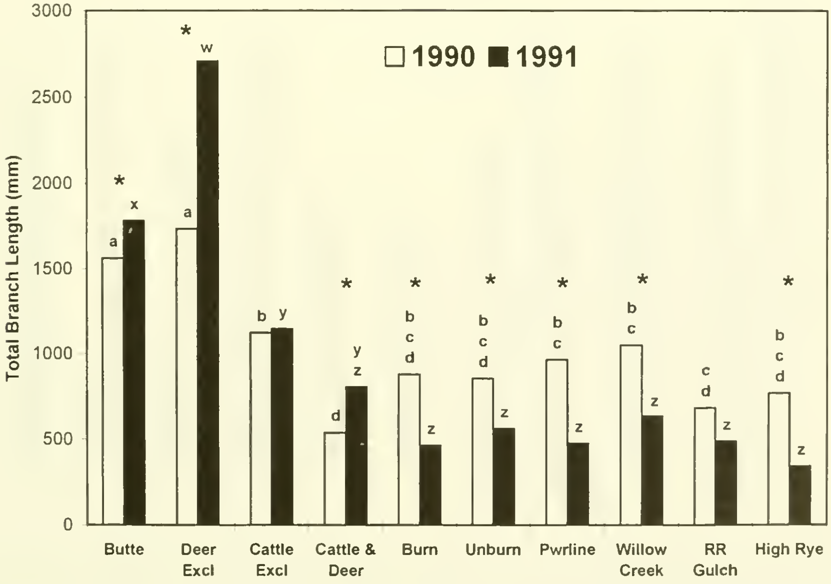

Fig. 2. Average total branch length (mm) of 1-, 2-, and 3-yr-old twig segments for plants ($n = 10$) at all study sites. The 2 unbrowsed sites are at left. Site-to-site, within-year differences (LSD, $P < 0.05$) are denoted by columns with unlike letters (abcd = 1990, wxyz = 1991). The asterik (*) denotes a site that had a year-to-year difference (Wilcoxon test, $P < 0.05$).

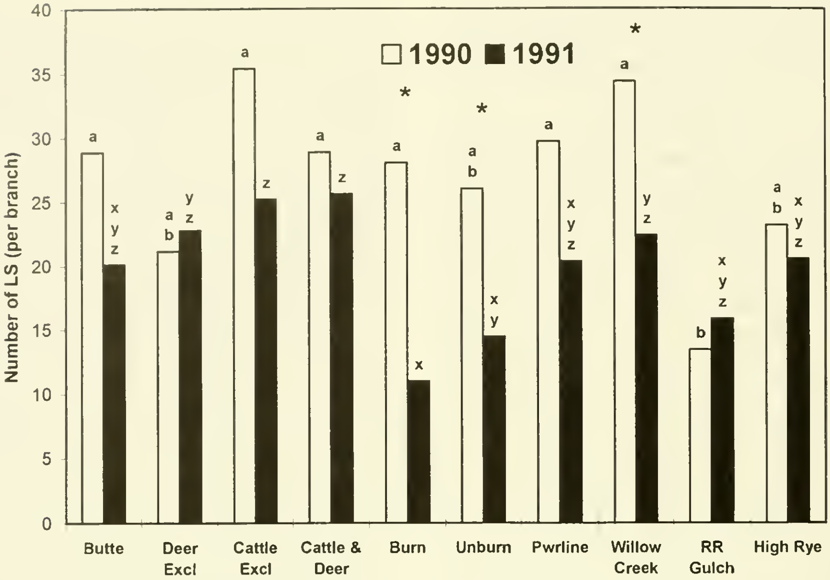

Fig. 3. Average number of long shoots (LS) per branch for plants ($n = 10$) at all study sites. The 2 unbrowsed sites are at left. Site-to-site, within-year differences (LSD, $P < 0.05$) are denoted by columns with unlike letters (ab = 1990, xyz = 1991). Only those sites denoted by an asterik (*) showed a year-to-year, within-site difference (Wilcoxon test, $P < 0.05$).

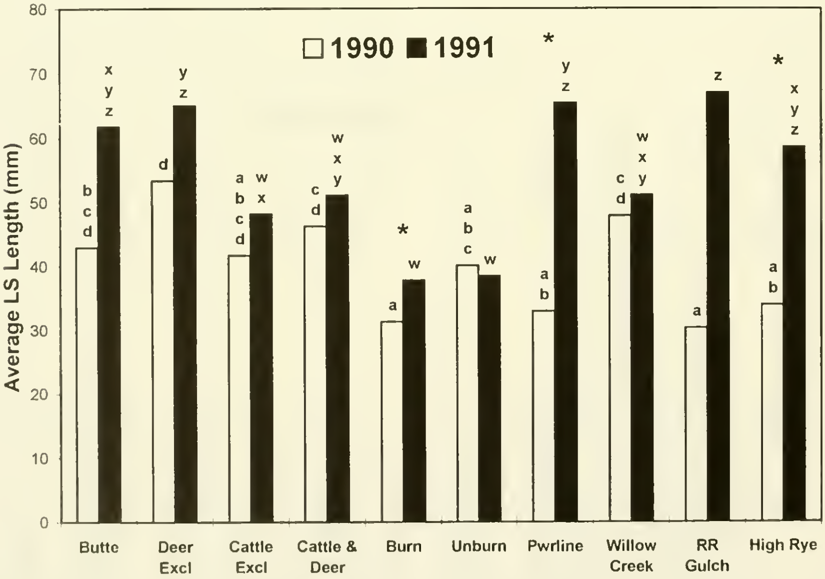

Fig. 4. Average ($n = 10$) long shoot (LS) length (total long shoot length divided by number of long shoots) per branch for all study sites. The 2 unbrowsed sites are at left. Site-to-site, within-year differences (LSD, $P < 0.05$) are denoted by columns with unlike letters (abcd = 1990, wxyz = 1991). Only those sites denoted by an asterik (*) showed a year-to-year, within-site difference (Wilcoxon test, $P < 0.05$).

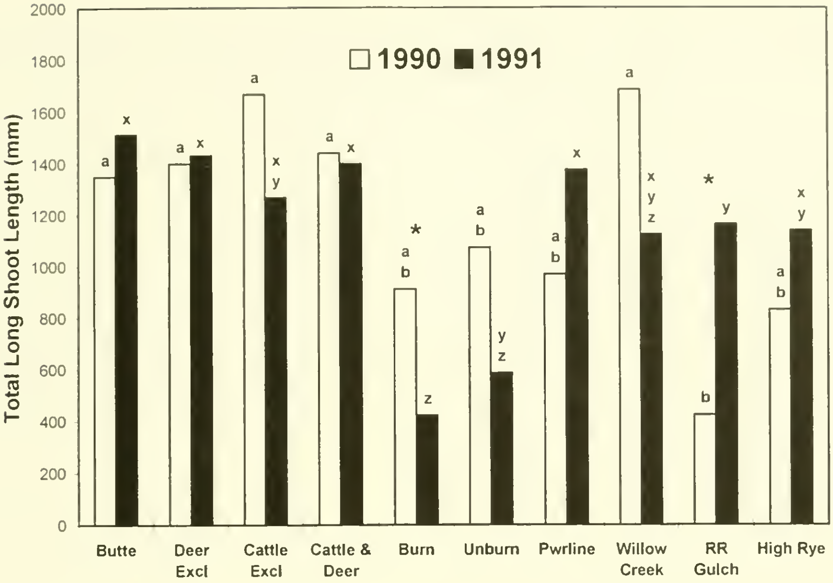

Fig. 5. Total long shoot length (mm) per branch (n = 10) for 1990 and 1991 for all study sites. The 2 unbrowsed sites are at left. Site-to-site, within-year differences (LSD, $P < 0.05$) are denoted by columns with unlike letters (ab = 1990, xyz = 1991). Only those sites denoted by an asterik (*) showed a year-to-year, within-site difference (Wilcoxon test, $P < 0.05$).

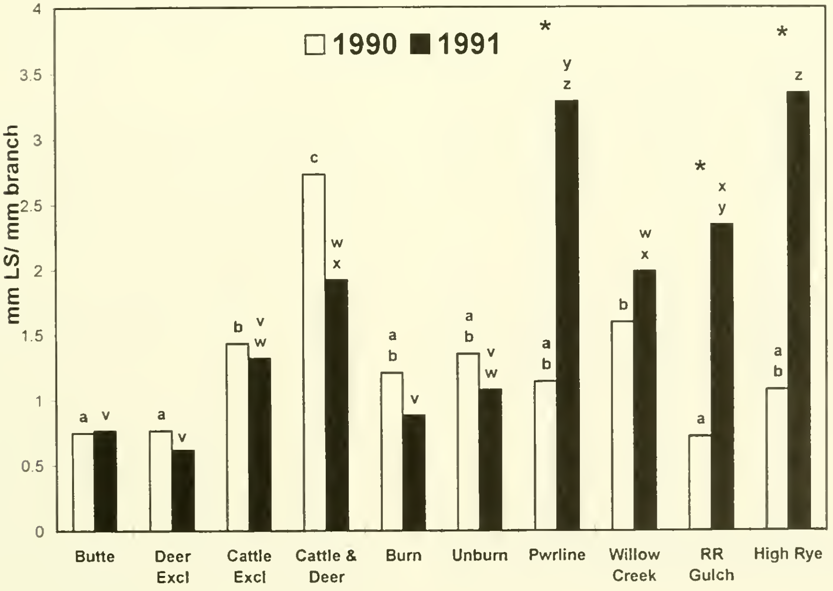

Fig. 6. Long shoot (LS) length per length of branch (mm/mm) (n = 10) in 1990 and 1991 for all study sites. The 2 unbrowsed sites are at left. Site-to-site, within-year differences (LSD, $P < 0.05$) are denoted by columns with unlike letters (abc = 1990, vwxyz = 1991). Only those sites denoted by an asterik (*) showed a year-to-year, within-site difference (Wilcoxon test, $P < 0.05$).

bitterbrush (Fraas et al 1992). The fact that both the growth rate and the browsing level (Table 2) were the same at the 2 sites suggests that browsers removed approximately the same amount of LS material from each branch at each site.

At the Dry Cottonwood exclosure site, LS length per unit of branch (Fig. 6) was greater on the Cattle + Deer site than the Cattle exclosure site in 1990, as was the Cattle exclosure greater than the totally unbrowsed Deer exclosure that year ($P < 0.01$). This tendency supports Tueller and Tower's (1979) stagnation theory, which predicts relatively higher growth rates at higher browsing levels. Reiner and Urness (1982) also reported that livestock grazing increased bitterbrush growth by reducing herbaceous competition during the growing season.

Overall we found only relatively minor variations in the characteristics measured among browsed unburned sites or between the 2 unbrowsed sites. However, our data indicate a fundamental difference in bud allocation patterns between browsed and unbrowsed bitterbrush plants and suggest that plants protected from browsing for many years should not be used as a standard for comparison with plants exposed to normal browsing pressures. Our results should increase knowledge of how bitterbrush responds to browsing. An understanding of the relationships between bitterbrush growth characters and management strategies should improve management for bitterbrush stands and the big-game winter ranges they often occupy.

Acknowledgments

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IDENTITY OF *MERTENSIA OBLONGIFOLIA* (NUTT.) G. DON (BORAGINACEAE) AND ITS ALLIES IN WESTERN NORTH AMERICA

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ABSTRACT.—The current status of *Mertensia oblongifolia* (Nutt.) G. Don and its allied taxa is surveyed. On the bases of continuously coherent morphological characters and/or regionally correlated variations, more than 30 taxa, including species, subspecies, varieties, and 1 forma, previously considered different from *M. oblongifolia*, are now placed under synonymy of this species. Those taxa currently known as *M. fusiformis* Greene, *M. bakeri* Greene, and *M. bakeri* var. *osterhoutii* Williams are among the new synonyms. Typification, taxonomy, and morphological problems of *M. oblongifolia* are discussed.

Key words: Mertensia oblongifolia, *typification, taxonomy, morphology, allied taxa.*

Nuttall (1834) described and depicted *Pulmonaria oblongifolia* from a collection of plants made by N.B. Wyeth in 1834 chiefly in the valleys of the Rocky Mountains, toward the sources of the Columbia River (corresponding to present-day states of Idaho and Wyoming).

As the Linnaean species of *Pulmonaria* (1753) in North America were placed within *Mertensia* (Roth 1797), *P. oblongifolia* Nutt. was transferred by Don (1838) into *Mertensia*. Except for a few additions, Don maintained Nuttall's description of *P. oblongifolia* for his species and was followed by de Candolle (1846), Gray (1875), and Coulter (1885).

M. oblongifolia was later treated as *Cerinthodes oblongifolium* (Nutt.) Kuntze (1891). Kuntze's contemporary botanists, such as Nelson (1899, 1900), Rydberg (1899, 1900), and Piper (1906), and subsequent workers on the genus *Mertensia* (Macbride 1916, Johnston 1932, Williams 1937, Higgins 1993) have recognized *M. oblongifolia* (Nutt.) G. Don as the correct name. In fact, *Cerinthodes oblongifolium* has remained inadequately known since Kuntze's time and seems never to have been mentioned again in the literature under *Mertensia* species in North America.

De Candolle (1846:91) pointed out that *M. oblongifolia* was one of the least known species of the genus *Mertensia*, but added no further discussion. However, de Candolle's report that the leaves were more or less pubescent beneath represents an important additional morphological feature in the taxon.

Macbride (1916) also argued that *M. oblongifolia* had been misinterpreted. He examined fragments of a specimen in the Gray Herbarium (GH) which were labeled, in Dr. Gray's hand, "*M. oblongifolia* Nutt.! ex sp. Wyeth! misit Durand 1861." He noted that pedicels of these fragments were very sparsely hispid; calyx divided nearly to the base, the lobes 5 mm long, linear-lanceolate; corolla-tube glabrous within, 10 mm long, limb 5 mm long; filaments as broad and as long as the anthers; style slightly exceeds. He concluded that the morphological characters of the fragments and Nuttall's description agreed perfectly. Williams (1937:124) also reported the above-mentioned fragments in his monograph: "a fragment marked in Dr. Gray's hand . . . is probably from the type specimen, Wyeth (G)." The word *probably* indicates doubt as to the identity of the fragment, and actually Williams' doubt leads to lectotypification of the fragment.

However, the key problems in this study concern the typification, taxonomy, and morphology of the species, questions that I have examined in connection with a proposed revision of the genus *Mertensia* in North America (Warfa in preparation).

Pulmonaria oblongifolia was described by Nuttall (1834:43) as follows: "Glabriuscula, caule simplici erecto, foliis lanceolato-oblongis obtusiusculis, superioribus acutis, floribus tubuloso-campanulatis paniculatis pedicellatis, calycibus abbreviatis, laciniis linearibus acutis ciliatis." Nuttall's description implies that he had seen a collection or a specimen with simple, erect, and subglabrous stem, etc. In his footnote Nuttall reported: "Stem . . . six to eight inches; lower leaves commencing some distance above the base of the stem . . . and all more or less pubescent above; panicle formed of axillary approximating clusters of flowers . . . ; corolla bright blue; style somewhat exserted." Nuttall thus explicitly stated that he studied a collection or at least a specimen with a complete habit "six to eight inches." His careful examination of the position of the lower leaves above the base of the stem and other described features further confirms his possession of an entire specimen. Don (1838:372) also mentioned a plant of 1/2 to 3/4 feet. Unlike both Nuttall and Don, Gray (1875:53), Macbride (1916:17), and Williams (1937:123) appear to have seen only the fragments of Nuttall's specimen at the Gray Herbarium (GH).

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I have seen Nuttall's plant collection at British Museum (BM) and the fragmentary specimen preserved at GH, the same scraps seen by Gray (1875), Macbride (1916), and Williams (1937). The fragmentary specimen is very poor, consisting mostly of dissected flowers and a single small leaf. As correctly pointed out by Macbride (1916), this fragmentary material is in accordance with Nuttall's description and the type specimen.

On the same sheet of the type specimen at BM are 2 other non-type specimens. Although these 2 latter specimens were collected much later and originate from different localities, they agree with *M. oblongifolia*. However, as duplicates of the type collection may possibly exist at the Herbarium of Kew Gardens (K) and/or elsewhere, I choose to designate the specimen deposited at BM as a lectotype and the fragmentary specimen preserved at GH as an isolectotype.

The synonymy of *M. oblongifolia* has a long, complicated history. *Mertensia longiflora* Greene (1898:261) was based on a collection made by Sandberg and Leiberg in 1893, tentatively identified and distributed as *M. oblongifolia*. It was placed in synonymy of *M. oblongifolia* by Piper (1906:479), who was followed by Macbride (1916:18). This synonymy was apparently rejected by Rydberg (1922:732), who kept *M. longiflora* a separate species. Rydberg's position was later supported by Jepson (1925:842), Williams (1937:136), Davis (1952:592), and John (1956:348). Both Williams and John not only recognized *M. longiflora* as a species, but also recognized a number of synonyms under this species. However, the status of *M. longiflora* has remained at the specific level since then.

M. foliosa Nelson (1899:243), erected from a collection made by Evanston and again tentatively identified and distributed as *M. oblongifolia*, was also placed in synonymy of *M. oblongifolia* by Macbride (1916:18–19). Macbride placed *M. nutans* Howell, *M. nevadensis* A. Nels., *M. pubescens* Piper, and *M. nutans* subsp. *subcalva* Piper together with *M. foliosa* in synonymy of *M. oblongifolia*, making 3 new combinations: *M. foliosa* var. *subcalva* (Howell) Macbr., *M. foliosa* var. *nevadensis* (A. Nels.) Macbr., and *M. foliosa* var. *pubescens* (Piper) Macbr. Except for a few modifications, Macbride's synonyms under *M. oblongifolia* were later supported by Williams (1937:123, 125, 130). Contrary to Macbride, Rydberg (1922: 732–733) treated *M. foliosa* and *M. nutans* as different species from *M. oblongifolia*. Similarly, Tidestrom (1925:467) considered *M. nevadensis*, *M. foliosa*, and *M. nutans* subsp. *subcalva* entities of their own and recognized *Pulmonaria oblongifolia* as the only synonym under *M. oblongifolia*.

Besides Macbride's observation on the relationship between *M. oblongifolia* and *M. foliosa*, Nelson (1909) studied the affinities between *M. fusiformis* Greene and *M. congesta* Greene on the one hand, and *M. bakeri* Greene, *M. laterifolia* Greene, and *M. amoena* A. Nels. on the other. Based on these affinities, Nelson established 3 new combinations: *M. papillosa fusiformis* (Greene) A. Nels., *M. bakeri amoena* (A. Nels.) A. Nels., and *M. bakeri laterifolia* (Greene) A. Nels. Nelson then placed *M. papillosa fusiformis* under *M. papillosa* Greene, while *M. bakeri amoena* and *M. bakeri laterifolia* were both placed under *M. bakeri*. He also placed *M. congesta* under *M. papillosa*, and *M. canescens* Rydb. under *M. bakeri*. Nelson's combinations and synonymy arrangements were apparently rejected by both Rydberg (1922: 734, 1932) and Tidestrom (1925:467), who treated *M. bakeri*, *M. fusiformis*, *M. amoena*, and *M. laterifolia* as species. While Rydberg placed *M. congesta* under *M. fusiformis*, *M. secundorum* Cockerell under *M. laterifolia*, and made nomenclatural transfer of *M. canescens* into *M. cana* Rydb., Tidestrom placed *M. paniculata* var. *nivalis* S. Wats. under *M. bakeri*. As did both Rydberg and Tidestrom, Williams (1937:100, 118) considered *M. bakeri* and *M. fusiformis* separate species each with a number of synonyms. Contrary to Rydberg, Williams placed *M. secundorum* under *M. lanceolata* (Pursh) A. DC. and *M. laterifolia* under *M. bakeri*.

Johnston (1932:84–85), aware of the strict ecological relationship between *M. foliosa* and its environments, studied this relationship carefully and affirmed that in response to the environment, this species exhibited 3 phases of morphological variation that correspond to (1) *M. foliosa*, (2) *M. foliosa* var. *subcalva*, and (3) *M. foliosa* var. *amoena* (A. Nels.) Johnston, respectively. Furthermore, he provided a more complete set of synonyms under each of these taxa and suggested that *M. foliosa* var. *subcalva* was better named *M. foliosa* var. *subcalva* f. *macbridei*, and *M. cusickii* Piper and *M. eplicata* Macbride as *M. foliosa* var. *amoena* f. *cusickii* (Piper) Johnston. *M. oblongifolia* was not mentioned in Johnston's paper.

In his monumental work, A Monograph of the Genus *Mertensia* in North America, Williams (1937) published the following new combinations under *M. oblongifolia*: *M. oblongifolia* var. *nevadensis* (A. Nels.) Williams, and *M. oblongifolia* var. *amoena* (A. Nels.) Williams. He recognized 26 synonyms under *M. oblongifolia* and its varieties (Williams 1937:123, 125, 130), as did Davis (1952:592). Higgins (1993:88) later found Williams' varieties of *M. oblongifolia* identical to the species and placed these infraspecific taxa into synonymy.

Despite the extensive literature available on the genus *Mertensia* in North America, the identity of *M. oblongifolia* and its relationship with *M. bakeri*, *M. fusiformis*, etc., have received little attention. Lack of information exchange and/or discordant opinions among early contributors may have overshadowed the significance of this relationship among the taxa in question.

The purpose of this paper is to review all literature available on the above-mentioned taxa and examine all type specimens of all taxa in this study. As a result of this review, I presently treat the species *M. oblongifolia*, *M. bakeri*, *M. fusiformis*, *M. foliosa*, and *M. amoena*, as well as most of their current synonyms, as a single morphologically variable but allied group (see Taxonomic Remarks and Variations). Therefore, *M. oblongifolia* is the only species recognized in this study, while *M. fusiformis*, *M. bakeri*, and *M. bakeri* var. *osterhoutii* Williams are among its new synonyms.

Although I have not yet examined the *M. longiflora* type specimen (Sandberg & Leiberg s. n.) at the herbarium of Notre Dame (ND), its current synonyms, such as *M. pulchella* Piper (1906), *M. pulchella* subsp. *glauca* Piper (1906), *M. horneri* Piper (1906), *M. longiflora* var. *horneri* Macbride (1916), and *M. longiflora* var. *pulchella* Macbride (1916), have been examined and found to be closely allied to *M. oblongifolia*. However, as I have not consulted the type material of *M. longiflora*, these taxa are not included in this study. Both *M. longiflora* and its synonyms will be placed either in synonymy to *M. oblongifolia* or as infraspecific taxa to it.

M. praecox Smiley, currently placed under *M. oblongifolia*, is now considered different from this species but rather close to *M. arizonica* Greene. Also, *M. stenoloba* Greene (1901) and *M. symphytoides* Greene (1901), both currently synonyms to *M. oblongifolia*, were not treated in this study because I was unable to examine the type specimens of these taxa, which are probably at the herbarium of ND as indicated by Williams (1937:126, 130) and/or elsewhere. However, *M. praecox*, *M. stenoloba*, and *M. symphytoides* will be treated together with the remaining taxa of the genus *Mertensia* in North America.

MATERIALS AND METHODS

This paper is based on a study of herbarium type material obtained on loan from BM, BRY, CAS, F, GH, ORE, RM, US, and WILLU herbaria (abbreviations according to Holmgren et al. 1990), as well as all literature available on the subject. In addition, I consulted a large set of *M. oblongifolia* collections, deposited at BRY and representing the states and counties in which the species occurs.

Only well-developed flowers, nutlets, and vegetative parts were used for measurements. Floral parts (when small) were measured under a Bausch & Lomb stereomicroscope after softening in ethanol alcohol; a ruler scaled in mm was used for measuring larger plant parts.

In this study I have generally followed taxonomic concepts commonly used in taxonomic revisions based mainly on herbarium material. I consider morphologically coherent units to be species; if considerable intraspecific variation is evident, I generally discuss it under Taxonomic Remarks and Variations. All synonyms are listed in chronological order under the species.

M. oblongifolia (Nutt.) G. Don, Gen. Hist. 4:372. 1838; de Candolle, Prodr. 10:92. 1846; S. Watson, U.S. Geol. Expl. 40th Par. (Bot. King's Exped.) 5:238. 1871; Gray, Proc. Am. Acad. 10:53. 1875; Coulter, Man. Bot. Rocky Mt. 262. 1885; Rydberg, Mem. N.Y. Bot. Gard. 1:336. 1900; Macbride, Contr. Gray Herb. N. S. No. 48:17. 1916; Tidestrom, Contr. U.S. Nat. Herb. 25:467. 1925; Williams, Ann. Mo. Bot. Gard. 24:123. 1937; Davis, Fl. Idaho 592. 1952; Higgins, Utah Fl. 88. 1993. *Pulmonaria oblongifolia* Nuttall, Jour. Acad. Nat. Sci. Phila. 7:43. 1834; G. Don, Gen. Hist. 4:372. 1838; de Candolle, Prodr. 10: 2. 1846. *Cerinthodes oblongifolium* (Nutt.) Kuntze, Rev. Gen. Pl. Pt. 2:436. 1891. Type locality: Idaho/Wyoming, Northern Andes, Towards Sources of Columbia River, Wyeth s. n. (BM! lectotype, GH! isolectotype, designated here).

M. paniculata (Ait.) G. Don var. *nivalis* S. Watson, U.S. Geol. Expl. 40th Par. (Bot. King's Exped.) 5:239. 1871, syn. nov. *M. nivalis* (Wats.) Rydberg, Mem. N.Y. Bot. Gard. 1:336. 1900, syn. nov. Type locality: Utah, Bear River Canyon, VIII.1869, Watson 844 (GH! holotype).

M. bakeri Greene, Pittonia 4:90. 1899, syn. nov.; Williams, Ann. Mo. Bot. Gard. 24:118. 1937. Type locality: Colorado, southern Colorado, summit of Mt. Hayden, 14.VII.1898, Baker, Earle & Tracey 576 (ND holotype, not seen, GH!, RM!, US! isotypes).

M. foliosa A. Nelson, Bull. Torr. Bot. Club 26:243. 1899, syn. nov; Williams, Ann. Mo. Bot. Gard. 24:125. 1937. Type locality: Wyoming, southwest Wyoming, on the sagebrush slopes in the foothills, 28.V.1897, Evanston 2951 (RM! holotype, GH! isotype).

M. fusiformis Greene, Pittonia 4:89. 1899, syn. nov.; Williams, Ann. Mo. Bot. Gard. 24:100. 1937. *M. papillosa fusiformis* (Greene) A. Nelson, Coult. and A. Nelson, Man. Ry. Mt. Bot. 421. 1909, syn. nov.; Williams, Ann. Mo. Bot. Gard. 24:100. 1937. Type locality: Colorado, Bob Creek, West La Plata Mountains, 28.VI.1898, Baker, Earle & Tracey 206 (ND holotype, not seen, F!, GH!, RM!, US! isotypes).

M. tubiflora Rydberg, Bull. Torr. Bot. Club 26:544. 1899, syn. nov.; Williams, Ann. Mo. Bot. Gard. 24:125. 1937. Type locality: Wyoming, Big Horn Mountains, headwaters of the Tongue River, VII.1898, Tweedy 119 (NY holotype, not seen, GH!, US! isotypes).

M. amoena A. Nelson, Bot. Gaz. 30:195. 1900, syn. nov.; Williams, Ann. Mo. Bot. Gard. 24:130. 1937. *M. bakeri amoena* (A. Nels.) A. Nelson, Coult. & A. Nelson, Man. Ry. Mt. Bot. 422. 1909, syn. nov.; Williams, Ann. Mo. Bot. Gard. 24:30. 1937. *M. foliosa* var. *amoena* (A. Nels.) Johnston, Contr. Arnold Arb. No. 3:85. 1932, syn. nov., Williams, Ann. Mo. Bot. Gard. 24:130. 1937. *M. oblongifolia* var. *amoena* (A. Nels.) L.O. Williams, Ann. Mo. Bot. Gard. 24.130. 1937, syn. nov. Type locality: Montana, Madison County, Monida, Glen Creek, Yellowstone Park, 16.VI.1899, Nelson & Nelson 5413, (RM! holotype, BRY!, GH!, US! isotypes).

M. intermedia Rydberg, Mem. N.Y. Bot. Gard. 1:335. 1900, syn. nov.; Williams, Ann. Mo. Bot. Gard. 24:125. 1937. Type locality: Montana, Bridger Mountains, 17–18.VI.1897, Rydberg & Bessey 4873 (NY holotype, not seen, GH! isotype).

M. congesta Greene, Pl. Baker. 3:17. 1901 (article not seen), syn. nov.; Williams, Ann. Mo. Bot. Gard. 24:100. 1937. Type locality: Colorado, Poverty Ridge, above Cimarron, 13.VI.1901, Baker 129 (ND holotype, not seen, GH!, RM!, US! isotypes).

M. lateriflora Greene, Pl. Baker. 3:18. 1901 (article not seen), syn. nov.; Williams, Ann. Mo. Bot. Gard. 24:118. 1937. *M. bakeri lateriflora* (Greene) Nelson, Coult. & Nels., Man. Ry. Mt. Bot. 432. 1909, syn. nov.; Williams 1937:118. Type locality: Colorado, Carson, western Colorado, 21.VII.1901, Baker 334 (GH! hololotype, RM!, US! isotypes).

M. nutans Howell, Fl. N. W. Am. 491. 1901 (article not seen), syn. nov.; Williams, Ann. Mo. Bot. Gard. 24:125. 1937. *M. foliosa* var. *subcalva* (Piper) Macbride, Contr. Gray Herb. N. S. No. 48:18. 1916. Type locality: Oregon, on high hills, near Goldendale, IV.1878 (20.IV.1882), Howell s. n. (ORE! holotype).

M. coronata A. Nelson, Bull. Torr. Bot. Club 29:403. 1902, syn. nov.; Williams, Ann. Mo. Bot. Gard. 24:125. 1937. Type locality: Wyoming, Sweetwater County, 9.VI.1900, Nelson 7071 (RM! holotype, GH!, ORE! isotype).

M. cusickii Piper, Bull. Torr. Bot. Club 29:643. 1902, syn. nov.; Williams, Ann. Mo. Bot. Gard. 24:130. 1937. *M. foliosa* var. *amoena* f. *cusickii* (Piper) Johnston, Contr. Arnold Arb. No. 3:85. 1932, syn. nov.; Williams, Ann. Mo. Bot. Gard. 24:130. 1937. Type locality: Oregon, Stein's Mts., eastern Oregon, 18.VI.1901, Cusick 2582 (article/specimen) (US! holotype, GH!, ORE!, RM! isotypes).

M. nevadensis A. Nelson, Proc. Biol. Soc. Wash. 17:96. 1904, syn. nov.; Williams, Ann. Mo. Bot. Gard. 24:125. 1937. *M. foliosa* var. *nevadensis* (A. Nels.) (A. Nelson) Macbride, Contr. Gray Herb. N. S. No. 48:19. 1916, syn. nov.; Williams, Ann. Mo. Bot. Gard. 24:125. 1937. *M. oblongifolia* var. *nevadensis* (A. Nels.) L.O. Williams, Ann. Mo. Bot. Gard. 24:125. 1937, syn. nov.; Davis 1952:592; Higgins 1993:88. Type locality: Nevada, Hunter Creek Canyon, 5 miles west of Reno, 16.V.1903, Kennedy & True 711 (RM! holotype).

M. myosotifolia Heller, Colo. Agr. Exp. Sta. Bull. (Fl. Colo.) 100:292. 1906 (article not seen), syn. nov; Williams, Ann. Mo. Bot. Gard. 24:118. 1937. *M. lanceolata* var. *myosotifolia* (Heller) Macbride, Contr. Gray Herb. N. S. No 48:15. 1916, syn. nov. Type locality: Colorado, Eagle County, Red Cliff, 26.VI.1900, Osterhout 2164 (MO lectotype, selected by Williams, not seen, GH! isolectotype).

M. nutans subsp. *subcalva* Piper, Contr. U.S. Nat. Herb. (Fl. Wash.) 11:479. 1906; Williams, Ann. Mo. Bot. Gard. 24:123. 1937. *M. foliosa* var. *subcalva* (Piper) Macbride, Contr. Gray Herb. N. S. No. 48:18. 1916; Williams, Ann. Mo. Bot. Gard. 24:123. 1937. *M. foliosa* var. *subcalva* f. *macbridei* (Macbr.) Johnston, Contr. Arnold Arb. 3:84. 1932, syn. nov.; Williams, Ann. Mo. Bot. Gard.

24:123. 1937. Type locality: Washington, Yakima Region, Rattlesnake Mts., 29.IV.1901, Cotton 328 (US! holotype, GH!, RM! isotypes).

M. pubescens Piper, Contr. U.S. Nat. Herb. (Fl. Wash.) 11:479. 1906, non de Candolle 1846, syn. nov.; Williams, Ann. Mo. Bot. Gard. 24:130. 1937. *M. foliosa* var. *pubescens* (Piper) Macbride, Contr. Gray Herb. N. S. No. 48:19. 1916; Williams, Ann. Mo. Bot. Gard. 24:130. 1937. Type locality: Washington, Douglas County, Waterville, 23.IV.1900, Whited 1214 (US! holotype, ORE! isotype).

M. refracta Nelson, Bot. Gaz. 56:69. 1913, syn. nov.; Williams, Ann. Mo. Bot. Gard. 24:118. 1937. Type locality: Colorado, Wagon Wheel Gap, 28.VII. 1912, Griffin 139 (RM! holotype, GH! isotype).

M. eplicata Macbride, Contr. Gray Herb. N. S. No. 48:16. 1916, syn. nov. Type locality: Idaho, Boise County, Dry Buck, 10.V.1911, Macbride 856 (RM! holotype).

M. nelsonii Macbride, Contr. Gray Herb. N. S. No. 48:19. 1916; Williams, Ann. Mo. Bot. Gard. 24:123. 1937. Type locality: Nevada, Elko County, Jarbidge, 9.VII.1912, Nelson & Macbride 1995 (RM! holotype, GH! isotype).

M. bakeri var. *subglabra* Macbride & Payson, Contr. Gray Herb. N. S. No. 49:66. 1917; Williams, Ann. Mo. Bot. Gard. 24:123. 1937. Type locality: Idaho, Custer County, Josephus Lakes, 3.VIII.1916, Macbride & Payson 3544 (GH! holotype, CAS!, RM! isotypes).

M. oblongifolia var. *nimbata* Macbride, Contr. Gray Herb. N. S. No. 53:18. 1918 (article not seen), syn. nov.; Williams, Ann. Mo. Bot. Gard. 24:130. 1937. Type locality: Montana, Bozeman, 18.V.1893, Gottschalch s. n. (GH! holotype).

M. cooperae Peck, Torreya 32:151. 1932 (article not seen), syn. nov; Williams, Ann. Mo. Bot. Gard. 24:130. 1937. Type locality: Oregon, Harney County, 6 miles west of Riley, VI.1922, Cooper 11127 (WILLU! holotype, GH! isotype).

M. bakeri var. *osterhoutii* Williams, Ann. Mo. Bot. Gard. 24:120. 1937, syn. nov. Type locality: Colorado, Grand County, Sulphur Springs, 8.VI.1906, Osterhout 3225 (RM! holotype, GH! isotype).

Perennial 10–50 cm tall, with fairly woody, thick, short, erect or vertical rootstocks, usually branched at the summit; roots numerous slender, fibrous, intermingled with few large woody ones, and the 1–several crowns closely covered or clothed with dead brown leaf bases and dead petioles; stems 1 or more from each elongated crown, straight and simple, ascending to erect, slightly to fairly conspicuously striate or angled, smooth or rough, glabrous or densely pubescent with fine, relatively long, spreading or closely appressed or crisped-retroflexed hairs. Leaves alternate, green, thick, occasionally ample, radical or lower leaves commencing some distance above the base of the stem, few, scattered, petiolate, the uppermost numerous or crowded at the summit, sessile to subsessile, with lamina linear-lanceolate to lanceolate-oblong or spatulate to narrowly oblong-ovate, rarely elliptic, 3–12 × 0.5–2.5(4.5) cm, attenuated or tapering, rarely rounded at the base, acuminate to obtuse, rarely rounded at the apex, entire, scabrous or sparsely to densely ciliate at the margins, glabrous to minutely scabrous on both sides, or sparsely to densely pubescent above, glabrous to scabrous beneath, or densely pubescent on both sides; midrib prominent; petiole winged, 6–12 cm long, glabrous or pubescent all over. Inflorescence congested, becoming panicled with age, with few branches to rather crowded, formed of axillary approximating clusters of flowers; peduncles up to 6 cm long; pedicels very slender and often drooping, 1–10 mm long, glabrous or pubescent; calyx divided nearly to the base, 3–8 mm long, enlarging in fruit, glabrous or pubescent, lobes 5, 2–5 mm long, narrowly linear to lanceolate-triangular, acuminate to acute, sparsely to densely ciliate or hispid at the margins. Plant hermaphrodite; flowers bright blue, occasionally subtended by lanceolate foliar bracts; corolla tubular-campanulate, up to 15 mm long, tube 5–12 × 3 mm, lobes 4–5 mm long, obtuse; stamens attached at the throat of corolla, free part of filaments 2–4 mm long, usually dilated, crests or appendages in the throat between the bases of the filaments conspicuous, with a 10-toothed ring at the base of the tube; anthers 1.2–2 mm long, oblong and straight; style 10 mm long, usually enclosed or somewhat exserted; nutlets 3 mm long, alveolar and white spotted, strongly muricate, rugose.

DISTRIBUTION.—*Mertensia oblongifolia* is widespread throughout the Mountain and Pacific states of North America.

HABITAT.—*M. oblongifolia* is known in clumps and moist open slopes. It is also found on plains, hillsides, and/or mountains with pine woods. It has an altitudinal range from 7800 to 13,000 feet (2377–3962 m).

TAXONOMIC REMARKS AND VARIATIONS.—*Mertensia oblongifolia* is one of the most morphologically variable species of the genus. The variation is probably correlated with geological and/or ecological responses. The subconical to conical, or shortly fascicled to cushion-shaped, or rarely tapering rootstock (caudex) of most type specimens of synonyms examined supports such variation. Basal and upper leaves, often monomorphic in shape, size, and pubescence for most synonyms of *M. oblongifolia*, or rarely dimorphic in some type specimens such as *M. cusickii* (Cusick 2582) and *M. eplicata*

(Macbride 856), both at RM, further confirm this variation. Regarding the indumentum, *M. oblongifolia* varies from entirely glabrous to completely pubescent.

VERNACULAR NAMES.—Bluebell, bluebells, spindle bluebell, western bluebell.

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ASTRAGALUS (LEGUMINOSAE): NOMENCLATURAL PROPOSALS AND NEW TAXA

Stanley L. Welsh[1]

ABSTRACT.—As part of an ongoing summary revision of *Astragalus* for the Flora North America project, several nomenclatural changes are indicated. Nomenclatural proposals include *A. molybdenus* var. *shultziorum* (Barneby) Welsh, comb. nov.; *A. australis* var. *aboriginorum* (Richardson) Welsh, comb. nov.; *A. australis* var. *cottoni* (M.E. Jones) Welsh, comb. nov.; *A. australis* var. *lepagei* (Hultén) Welsh, comb. nov; *A. australis* var. *muriei* (Hultén) Welsh, comb. nov.; *A. subcinereus* var. *sileranus* (M.E. Jones) Welsh, comb. nov.; *A. tegetarioides* var. *anxius* (Meinke & Kaye) Welsh, comb. nov.; *A. ampullarioides* (Welsh) Welsh, comb. nov.; *A. cutleri* (Barneby) Welsh, comb. nov.; and *A. laccoliticus* (M.E. Jones) Welsh, comb. nov. Proposals of new taxa include *Astragalus* sect. Scytocarpi subsect. Microcymbi Welsh, subsect. nov., and *A. sabulosus* var. *vehiculus* Welsh, var. nov. A lectotype is selected for *Phaca australis* L.

Key words: Astragalus, *nomenclature, new taxa.*

Astragalus, with more than 350 species and a great many infraspecific taxa, is perhaps the largest genus of North American plants. Its complexity has long been recognized as evidenced by its tangled nomenclatural history. Experts and others interested in this vast genus have encountered enormous problems in dealing with it, especially prior to 1964. In that year Rupert Barneby, in his classic account (in my opinion, the most impressive taxonomic work of the century), untied the Gordian knot of nomenclature, typification, and classification of *Astragalus* for North America. Regardless of when a taxonomic work is attempted, there will be shortfalls in information availability, in adequacy of specimens, in confluence of data from disparate regions, and in overall understanding through time. Despite those problems, the Atlas of North American *Astragalus* (Barneby 1964) will stand for all time as a remarkable attempt to understand this huge genus and as a tribute to Barneby's genius.

It is hoped that the proposals discussed herein represent some helpful minor additions to the work by Barneby, whose treatment is reflected in a large manuscript now in preparation for the Flora North America (FNA) project by S.L. Welsh and R. Spellenberg. Included below are sufficient portions of that treatment to allow the current proposals to be put into perspective and to be used by workers prior to appearance of the entire manuscript within the FNA publication schedule. Format is as understood for the FNA publication; order of treatment is phylogenetic as per Barneby, or as per present modification.

Astragalus molybdenus **Barneby**, Leafl. W. Bot. 6:70. 1950. **Leadville milkvetch.**

Low, loosely matted, shortly caulescent perennials, 0.5–6 (14) cm long, from extensively branching subterranean caudex branches. **Pubescence** strigulose-pilosulous, basifixed. **Stems** largely subterranean, the aerial tips prostrate or ascending. **Stipules** 2–5 mm long, all connate-sheathing. **Leaves** 1.5–7 cm long; leaflets (9) 17–25, 2–10 mm long, ovate, ovate-oblong, or elliptic, obtuse, mostly crowded, folded or involute. **Peduncles** 1–3 (6.5) cm long; racemes loosely 3- to 6-flowered, the axis scarcely elongating, 3–10 (15) mm long in fruit; bracts 2.5–5 mm long; pedicels 0.5–2 mm long; bracteoles 0–2. **Calyx** 5.2–7 mm long, the tube campanulate, 3–4.2 mm long, the teeth subulate, 2–3 mm long. **Flowers** 10.7–12.5 mm long, pink-purple, lilac, or whitish, the banner veined and suffused with lilac, recurved through ca 45°, the keel tip maculate. **Pods** ascending, sessile or nearly so, 7–11 (12) mm long, 3–3.5 mm thick, obliquely ovoid or ovoid-ellipsoid, somewhat incurved, 1-loculed, strigulose. **Ovules** 6.

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1. Leaflets of upper leaves 17–25; racemes 3- to 6-flowered; plants of central Colorado and Teton Co., Montana . . . . var. *molybdenus*
— Leaflets of upper leaves 9–17; racemes mostly 1- or 2 (exceptionally 3)-flowered; plants of the Salt River Range, Lincoln Co., Wyoming . . . . var. *shultziorum*

Astragalus molybdenus **var.** ***molybdenus***

[based on: *A. plumbeus* Barneby, Leafl. W. Bot. 5:195. 1949, non *A. plumbeus* Gontscharow].

Dwarf alpine plants, the caudex deeply subterranean, the branches rhizomatous. **Stipules** 2–5 mm long. **Leaves** 1.5–7 mm long, (the uppermost) with 17–25 leaflets, 2–10 mm long. **Peduncles** 1–3 (6.5) cm long, the racemes 3- to 6-flowered. **Calyx** 5.2–7 mm long, the tube campanulate, 3–4.2 mm long, the teeth subulate, 2–3 mm long. **Flowers** 10.7–12.5 mm long, pink-purple, lilac, or whitish, the banner recurved through ca 45°. **Pods** rather abruptly contracted into a short beak. **Ovules** 6. *Type: "Colorado: . . . about 4 miles east of Leadville, Lake County . . . Ripley & Barneby No. 9994 . . . west slope of Mosquito Pass, east of Leadville, No. 10045"; syntypes CAS!; isosyntypes GH!, K, NY!, POM!, RM!, RSA, US, WTU.*

Flowering July, August. Alpine tundra community at 3780–3965 m, along the Continental Divide, along the boundaries between Gunnison-Pitkin, Lake-Park, and Park-Summit counties, in central Colorado, and disjunct in Teton Co., Montana.

Astragalus molybdenus **var.** ***shultziorum*** **(Barneby) Welsh comb. nov.**

[based on: *A. shultziorum* Barneby, Brittonia 33:156. 1958].

Dwarf alpine plants, the caudex deeply subterranean, the branches rhizomatous. **Stipules** 2–3 mm long. **Leaves** 1.5–7 (8) cm long, the uppermost with 9–15 (17) leaflets, 2–7 mm long, lance- or ovate-elliptic, obtuse to acute, mostly distant, flat or loosely folded. **Peduncles** (0.5) 1–4 cm long, the racemes (usually 2-) 1- to 3-flowered. **Calyx** (5) 5.7–6.7 mm long, the tube campanulate, (3) 3.4–4 mm long, the teeth subulate, 1.8–3.3 mm long. **Flowers** 11–12 mm long, whitish lavender tinged, the banner veined and suffused with lilac, recurved through ca 50°, the keel tip maculate. **Pods** tapering to an elongate beak. **Ovules** 8 or 9. *Type: "Wyoming. Lincoln County: stony hilltop, 9500 ft, mountains near Cottonwood Lake, E of Smoot, 31 Jul 1923 (fl), E.B. Payson & G.M. Armstrong 3651," holotype POM!; isotypes MO, NY!, WYO.*

Flowering July, August. Alpine tundra and krummholz or on talus, at 2865–3150 m, in Salt River Range, Lincoln Co., Wyoming.

Plants of the 2 varieties are essentially identical in aspect, but the features noted in the key appear to be substantial diagnostic ones.

Astragalus australis **(L.) Lam., Fl. Fr. 2:637. 1778. Subarctic milkvetch.**

[*Phaca australis* L., Mant. Pl. 1:103. 1767].

Moderate, caulescent perennial, (10) 20–30 cm tall, from a superficial caudex. **Pubescence** silky-strigose, villous, or villous-tomentose, basifixed. **Stems** erect or ascending, few to several. **Stipules** (1) 2–7 (11) mm long, often veined, semicoriaceous, at least the lowermost connate-sheathing. **Leaves** (1) 2–7 (10) cm long; leaflets (5) 7–15, 3–28 (35) mm long, 1–7 (8) mm wide, oblong, linear-elliptic, elliptic, or linear-oblong, acute, villous to glabrate on both sides. **Peduncles** 2–10 (14) cm long; racemes 2- to 40-flowered, rather compact and ascending at anthesis, the axis 1–15 cm long in fruit; bracts 1.2–5 mm long; pedicels 0.8–3.5 mm long; bracteoles 0. **Calyx** 3.7–6.4 mm long, the tube 2.1–5 mm long, campanulate, villous, the teeth 1–3 mm long, subulate. **Flowers** 7.5–14.5 mm long, ochroleucous or suffused with pink, the wing petals bilobed apically, the banner recurved through 40–50°. **Pods** pendulous, stipitate, the stipe 2.5–8 (10) mm long, the body obliquely and narrowly elliptic in outline, 13–27 mm long, 3–9 (11) mm wide, semibilocular, the septum 0–0.6 mm wide, glabrous or pubescent. **Ovules** 8–16; 2n = 16, 32, 48. *Type: "Habitat in alpinis Helvetiae, Italiae, Gallo Provinciae," lectotype here designated, illustration of "Astragaloides Alpina supina glabra, foliis auctioribus," in Tilli, Cat. Pl. Hort. Pisani 19. 5. 14. f. 1. 1723!*

American materials of *A. australis* are portions of a vast circumboreal species complex demonstrating great variability, beginning with the typical material in southern Europe and extending eastward. Asiatic plants passing under the names *A. tugarinovii* Basilevskaja, *A. gorodkovii* Jurtsev, *A. tolmaczevii* Jurtsev, and *A. kolymensis* Jurtsev (Korobkov et al. 1986) belong to this complex, with the entities having the same degree of morphological integrity (or lack thereof) as the American materials. Varietal segregation within the North

American variants has been based on differences in pubescence, leaflet shape, and pod size and shape. Several varieties have been proposed, with the best summary that of Barneby (1964:137). Often great variation occurs within a single population, but some of the proposed taxa have apparent geographical correlation; others are haphazard or represent a mere continuum. Many of the variants can be determined mechanically on a 2n basis, essentially as summarized by Barneby. It will be possible by using the following key to identify the most conspicuous morphological, but admittedly transitional, variants. Variability is the rule within the species, and a more detailed segregation, though possible, might separate morphologically similar individuals—not taxa. Perhaps even the following proposals do not represent taxa, per se, but there are hints of correlation of some features with geographical and ecological distributions.

1. Flowers 7.5–11 (12) mm long; calyx 3.5–5.9 mm long; plants of broad distribution.

2. Leaves petiolate; plants from eastern Alaska and Yukon . . . . var. *muriei*

2. Leaves sessile, the lower pair of leaflets arising from the stipules, appearing as if foliose stipules; plants from southern Yukon southward (Rocky Mts. and Olympics).

3. Pods 3–7 (9) mm broad, seldom much if at all bladdery; peduncles 6.5–15 cm long; plants widely distributed . . . . var. *aboriginorum*

3. Pods 7–9 (11) mm broad, bladdery inflated; peduncles 3–6.5 cm long; plants known only from the Olympic Mts., Washington . . . . var. *cottoni*

1. Flowers 11.5–13.8 (14.5) mm long; calyx 5.7–6.5 mm long; plants from west central to northern Alaska, east to northern Yukon and Northwest Territories. . . . . var. *lepagei*

Astragalus australis var. *muriei* (Rydberg) Welsh, comb. nov.

[based on: *A. aboriginorum* var. *muriei* Hultén, Fl. Alaska & Yukon 1080. 1947; *Atelophragma lineare* Rydberg, Bull. Torrey Bot. Club 40:50. 1913].

Stems 7–35 cm long, ascending. **Leaves** (2) 3–6.5 cm long; leaflets (7) 9–15, 6–15 mm long, linear to narrowly elliptical, acute to obtuse, glabrous to strigulose-pilosulous or villous. **Peduncles** 2.5–11 cm long, typically longer than the leaf. **Racemes** rather densely to somewhat loosely (6) 8- to 21-flowered, the axis 1.5–9.5 cm long in fruit. **Calyx** 4.2–5.5 mm long, the tube 2.4–2.7 mm long, campanulate, strigulose to villous, the teeth 1.1–2.5 mm long, narrowly subulate. **Flowers** 8.5–9.5 mm long, whitish to purplish. **Pod** stipe 4–6 mm long, the body obliquely ellipsoid to narrowly oblong, 11–24 mm long, 4–7 mm wide, the valves glabrous to occasionally strigose. *Type: Alaska, "Central Yukon R. distr.: Porcupine R., 45 miles from its mouth, O.J. Murie 2162, June 26, 1926," holotype S!*

Flowering June, July. Mountain slopes, ridge crests, meadows, and less commonly on gravel bars, at ca 200–860 m, east central Alaska, and British and Barn mountains of northern Yukon, and in the Yukon River Valley and vicinity of Kluane National Park, southwest Yukon.

Diagnostic criteria that would separate specimens from northern Yukon, those with petiolate leaves, from plants at the type locality of *A. australis*, sens. str., in the Alps of southern Europe, are not resolved herein. They appear to be essentially identical. Petiolate specimens occur throughout the range of var. *muriei* as here interpreted. The type of this variety has strigulose pods, unusual in plants from the Arctic, but pubescence does not seem to have diagnostic value within the group. Many of the *muriei* specimens were from ridge tops, especially in northern Yukon, with a smaller number from stream gravels (the apparent preferred habitat of most of var. *lepagei*, q.v.). Plants from southwestern Yukon are more nearly uniform and belong to the "*linearis*" phase, whose type is from the famous Lake Labarge (now "Laberge," collected by J.B. Tarlton in 1899, holotype NY!, isotype US!).

Astragalus australis var. *lepagei* (Hulten) Welsh comb. nov.

[based on: *A. lepagei* Hulten, Fl. Alaska & Yukon 1761. 1950; *A. tugarinovii* Basilevskaja; *A. tolmaczevii* Jurtsev].

Stems (8) 24–40 cm long, sprawling to ascending. **Leaves** 3–9 cm long, sessile or definitely petiolate; leaflets (5) 9–15, 6–33 mm long, elliptic to lanceolate, lance-oblong, linear-lanceolate or linear, acute to apiculate, glabrous to strigulose, pilosulous, or villous. **Peduncles** (4) 4.5–10 cm long, typically longer than the leaf. **Racemes** rather densely to loosely 8- to 29 (32)-flowered, the axis 3–14 cm long in fruit. **Calyx** (4.7) 4.8–6.5 cm long, the tube 2.8–5 mm long, campanulate to deeply so, black strigulose to villous, the teeth (1) 1.4–2.4, narrowly subulate. **Flowers** (9.5) 11.5–13.8 mm long, whitish to purplish. **Pod** stipe (3) 5–7 mm long, the body obliquely ellipsoid to narrowly oblong, (10) 15–30 mm long, (3) 6–8.5 mm wide, the valves typically glabrous. *Type: "Arctic Coast distr.: Umiat, July 29, 1948, Lepage 23601," holotype S!*

Flowering June, July. Often on gravel bars, but also on spits, beaches, and less commonly on ridge crests in mixed tundra, from near sea level to 350 m, from coastal western Alaska, along the northern and southern slopes of the Brooks Range, south to near the 65th parallel, and east to the ranges of northern Yukon and continental and insular Northwest Territories, Canada.

Plants from northern Alaska, Yukon, and Northwest Territories are variable also but seem to revolve about a group of plants from sand bars, spits, and beaches with overall larger flowers and broader pods. Well-developed, large-flowered collections from the Coville River at Umiat were sufficiently distinctive that Hultén (1950:1761) compared them with *A. harringtonii* (Rydberg) Hultén of the *robbinsii* complex. Even those large-flowered specimens are part of a continuum, with small-flowered plants forming the other extreme, especially in coastal western Alaska. In northern Yukon the large-flowered material is transitional with smaller flowered plants assigned herein to var. *muriei*.

Astragalus australis var. *aboriginorum* (Richardson) Welsh, comb. nov.

[based on autonym of: *A. aborigin[or]um* var. *fastigiorum* M.E. Jones, Rev. Astrag. 135. 1923, i.e., *A. aboriginorum* Richardson in Franklin, Jour., Append. 746. 1822; *Phaca glabriuscula* Hooker, Fl. Bor. Amer. 1:144. 1831; *A. glabriusculus* var. *major* A. Gray, Proc. Acad. Nat. Sci. Philadelphia 1863:60. 1863; *A. australis* var. *glabriusculus* (Hooker) Isely, Syst. Bot. 8:421. 1983; *A. forwoodii* S. Watson; *A. richardsonii* Sheldon; *Atelophragma wallowense* Rydberg; *Atelophragma herriotii* Rydberg; *Astragalus scrupulicola* Fernald & Weatherby].

Stems 10–50 cm long, ascending. **Leaves** sessile, 1–7 (10) cm long; leaflets 5–15, 3–27 (35) mm long, linear to oblong, lanceolate, or elliptical, acute to obtuse, glabrous to strigose or villous. **Peduncles** 6.5–15 cm long, typically longer than the leaf. **Racemes** rather densely 6- to 40-flowered, the axis 1.5–15 cm long in fruit. **Flowers** 7–12.5 mm long, whitish to purplish. **Pod** stipe 2.5–8 mm long, the body obliquely ellipsoid to narrowly oblong, 10–30 mm long, 3–7 mm wide, the valves glabrous to occasionally strigose. **Ovules** 8–16. *Type: "Vallies of the Rocky Mountains," Drummond, holotype K.*

Flowering May to July. Gravel bars, stony shores, talus, ridge crests, and meadows, growing with an immense array of plant species through its huge geographical range, at ca 20–3630 m; Yukon east to Gaspé, and south to Oregon, Nevada, central and northern Utah, Colorado, and western South Dakota.

The var. *aboriginorum* consists of the aggregation of variants distributed in the mountains and valleys from northern British Columbia southward, exclusive of the isolated var. *cottoni*. Separation of the "*linearis*" phase in the Yukon from the northernmost outliers of var. *aboriginorum* is rather tenuous. However, most of var. *muriei* (including the *linearis* phase) have petiolate leaves, at least at the lower nodes. And the great body of specimens south along the cordillera have sessile leaves, but include a great many variable specimens, often growing intermixed within the same populations. Further segregation seems futile at present.

It is unfortunate that the synonymy, already overcrowded, should have yet another name. Insistence on priority of autonyms in recent codes of botanical nomenclature has led to such clutter. In this case the earliest autonym available for the geographically most extensive American variety is "*aboriginorum*." Barneby (1964, et subsequent) cited the name as "*aboriginum*" but later used the suffix *-orum* for taxa named by him.

Astragalus australis var. *cottoni* (M.E. Jones) Welsh, comb. nov. Cotton's milkvetch.

[*A. cottoni* M.E. Jones, Rev. Astrag. 135. 1923, nom. nov. pro: *A. olympicus* Cotton, Bull. Torrey Bot. Club 29:573. 1902, non *A. olympicus* Pallas, 1800; *A. australis* var. *olympicus* (Cotton) Isely, Syst. Bot. 8:421. 1983, nom. illeg.; *Atelophragma cottoni* (M.E. Jones) Rydberg].

Stems 1–1.7 dm long, decumbent to ascending. **Leaves** (1.5) 2–5.5 cm long; leaflets 9–15 (17), 4–16 mm long, linear-elliptic to elliptic-oblanceolate, acute to subacute, villosulous or glabrate above. **Peduncles** 3–6.5 cm long, typically equaling or somewhat longer than the leaf. **Racemes** rather densely 11- to 21-flowered, the axis 2–6 cm long in fruit. **Flowers** 10–12.2 mm long, creamy white. **Pod** stipe 3–5 mm long, the body semi-ellipsoid, bladdery inflated, 20–25 mm long, 7–9 (11) mm thick, the valves glabrous. **Ovules** 10–15. *Type: "Olympic Mts., Clallam County, July, 1900, A.D.E. Elmer"; holotype WS; isotypes NY!, ORE, P, US!.*

Flowering June, July. Ridge tops and talus, on granite at 1380–1680 m in the Olympic Mts., Clallam Co., Washington.

This is the most distinctive of the variants within the *australis* complex in North America, hence its recognition previously at specific level. It is isolated by many kilometers from other taxa in the complex.

Astragalus subcinereus **A. Gray**, Proc. Amer. Acad. 13:366. 1878. **Siler's milkvetch.**

Low, caulescent perennial, 14–90 cm long, radiating from a subterranean, branching caudex. **Pubescence** villosulous or hirsutulous, basifixed. **Stems** few to several, prostrate to weakly ascending, buried for a space of (1) 2–10 (15) cm. **Stipules** 1.5–6.5 mm long, at least some connate-sheathing. **Leaves** 1.5–8.5 cm long; leaflets 9–23, 2–16 mm long, 1–8.5 (10) mm wide, oblong to oblanceolate or obovate, obtuse, emarginate, or retuse, villosulous on both surfaces or glabrate above. **Peduncles** 1.5–10 cm long; racemes 5- to 37-flowered, the flowers ascending to declined at anthesis, the axis 1–7 cm long in fruit; bracts 1–3 mm long; pedicels 0.5–2.5 mm long; bracteoles 0–1. **Calyx** 3.4–6.3 mm long, the tube 2.3–3.6 mm long, campanulate, villosulous, the teeth 0.9–2.9 mm long, subulate. **Flowers** 6–11 mm long, ochroleucous and commonly suffused with purple. **Pods** spreading to declined, subsessile, inflated, ovoid-ellipsoid to ellipsoid, 12–27 mm long, (3.5) 6–13 mm wide (when pressed), subterete to dorsoventrally compressed, thinly villosulous, mottled. **Ovules** 10–20.

Much of the material from Kane, Garfield, and Washington counties, Utah, differs from the typical plants in Mohave Co., Arizona, in being more leafy (the leaflets 4–10 mm broad), in having longer stems (3–7 dm long), and in having more firmly walled pods (15–28 mm long, and 6–10 [13] mm thick). These Utah plants belong, sens. str., to var. *caraicus* M.E. Jones (i.e., the autonym var. *sileranus*). Although the features are weak and overlapping, they form a syndrome of characteristics indicative of an evolutionary trend and are herein treated at varietal level, bringing to 3 the number of taxa within the species.

1. Mature pods ovoid-ellipsoid, (5) 6–13 mm wide; flowers 5–9 mm long; stems mostly 14–70 cm long; plants commonly of sedimentary gravels, sometimes from igneous substrates, southern Utah and northern Arizona.
    2. Pods ellipsoid, turgid, but not bladdery inflated, more than twice as long as broad (or if shorter, then differing otherwise; stems prostrate, radiating from the root crown; plants of Garfield, Kane, Iron, and eastern Washington counties, Utah, and Lincoln Co., Nevada . . . . var. *sileranus*
    2. Pods ovoid or ovoid-ellipsoid, bladdery inflated, less than twice as long as broad; stems ascending or less commonly prostrate; plants of Coconino and Mohave counties, Arizona, and Lincoln Co., northern Nevada . . . . var. *subcinereus*
1. Mature pods elliptic-oblong to oblong, 3.5–6 (7) mm wide; flowers 8.5–11 mm long; stems 40–90 cm long; plants of igneous gravels in eastern Sevier and western Emery counties, Utah . . . . var. *basalticus*

Astragalus subcinereus **var. *subcinereus***

Plants with stems to 5 dm long or less, with mature pods relatively broad, mainly 6–13 mm wide, and otherwise differing as in the key. *Type: "Mokiak Pass in the northwestern part of Arizona, near the Utah boundary, Dr. E. Palmer, 1877," holotype GH!; isotypes K, MO, NY!, PH, US!*

Ponderosa pine, pinyon-juniper, and sagebrush communities at 1670–2410 m, in Garfield, Iron, Kane, and Washington counties, Utah; Lincoln Co., Nevada; and Mohave and Coconino counties, Arizona.

Astragalus subcinereus **var. *sileranus*** **(M.E. Jones) Welsh, comb. nov. Siler's milkvetch.**

[based on the autonym of *A. sileranus* var. *cariacus* M.E. Jones, Proc. Calif. Acad. Sci. II. 5:642. 1895; *A. sileranus* M.E. Jones, Zoë 2:242. 1891; *Phaca silerana* (M.E. Jones) Rydberg].

Plants prostrate, radiating from a root crown, with stems to 6 dm long, often conspicuously flexuous. **Pods** ellipsoid, mostly more than twice longer than broad (or if shorter, less than 7 mm wide and the texture leathery). *Type: "Collected by me [M.E. Jones] on June 23, 1890, in Sink Valley, southern Utah, at about 7000 feet altitude," holotype POM!, isotypes CAS!, GH!, MO, NY!, US!*

Flowering May, June. Ponderosa pine, aspen, oak, pinyon-juniper, and mixed mountain brush communities at 1700–2750 m, in Garfield, western Kane, eastern Washington, and Iron counties, Utah; and Lincoln Co., Nevada.

Astragalus subcinereus **var. *basalticus*** **Welsh**, Great Basin Naturalist 38:302. 1978. **Basalt milkvetch.**

Plants with stems to 8 dm long, with mature pods narrow, mainly 3.5–6 (7) mm wide, and otherwise differing as in the key. *Type: "Utah, Sevier Co., 16 km S of Fremont Junction, S.L. Welsh, D. Isely, & G. Moore 6447, 23 July 1967," holotype BRY!, isotype ISC!*

Flowering May, June. Pinyon-juniper and ponderosa pine communities at 1380–2430 m in western Emery and eastern Sevier counties, Utah.

Specimens of var. *basalticus* grow sympatrically with *A. flexuosus* var. *diehlii* (M.E. Jones) Barneby. When material of the latter variety is robust, it approaches var. *basalticus* in habit, but not in pod and flower size. Indicated, however, is a close alignment between the 2 taxa, and var. *basalticus* might possibly be treated within an expanded *A. flexuosus* var. *diehlii* or within *A. subcinereus*. The more robust nature of var. *basalticus* precludes alignment with *A. flexuosus*, however.

Astragalus sect. Scytocarpi subsect. Microcymbi Welsh, subsect. nov.

[based on: *A. microcymbus* Barneby, Amer. Midl. Naturalist 41:499. 1949.]

Perennial, caulescent, with a shortly subterranean caudex. **Pubescence** basifixed. **Stipules** dimorphic, at least the lowermost connate-sheathing. **Leaves** with 9–15 oblong-obovate or obovate-cuneate, emarginate, folded leaflets. **Racemes** loosely (3) 7- to 14-flowered. **Calyx** 2.2–2.6 mm long, the tube 1.4–1.9 mm long, the teeth 0.5–0.7 mm long. **Flowers** 5.6–5.8 cm long. **Pods** 6–9 mm long, obscurely stipitate, almost or quite bilocular. **Ovules** 4–6.

The subsection is monotypic.

Astragalus microcymbus Barneby, Amer. Midl. Nat. 41:499. 1949. Skiff milkvetch.

Slender, diffuse, caulescent perennial, 25–60 cm tall, from a shallowly buried caudex. **Pubescence** strigulose to subvillosulous, basifixed. **Stems** prostrate or weakly ascending, subterranean for a space of 1–3 cm. **Stipules** 1.5–3 mm long, at least the lower ones connate. **Leaves** (1.5) 2–4 cm long, shortly petioled or the uppermost subsessile; leaflets 9–15, oblong-ovate or oblong-cuneate, 3–9 mm long, emarginate. **Peduncles** (0.8) 1.5–3.5 cm long, variously hairy; racemes loosely (3) 7- to 14-flowered, the axis (1) 2–6.5 cm long in fruit. **Flowers** 5.6–5.8 mm long, whitish tinged with lilac, the banner recurved through ca 45°. **Calyx** 2.2–2.6 mm long, the tube 1.4–1.9 mm long, campanulate or obconic-campanulate, strigulose with white and fuscous hairs, the teeth 0.5–0.7 mm long, subulate. **Pods** pendulous, obscurely stipitate, the stipe ca 0.4 mm long, concealed by the calyx, the body ellipsoid or lance-ellipsoid, 6–9 mm long, (2.5) 3–3.3 mm thick, obcompressed, the valves white-villosulous, almost or quite 2-loculed, the septum 0.8–1.3 mm wide. **Ovules** 4–6. *Type: "Colorado: . . . four miles west of Gunnison, Gunnison Co., . . . 20 July 1945, fl. & fl., Ripley & Barneby No. 7179"; holotype CAS!; isotypes COLO, GH!, RSA.*

Flowering July, August. Dry, sandy and gravelly sites in sagebrush, at 2310–2640 m, in hills west and southwest of Gunnison, Colorado.

Despite conjecture that the skiff milkvetch might represent a recent introduction from unknown source, its ecological placement is not unlike that of numerous other species of *Astragalus*. There is no reason to believe that it is other than indigenous and endemic. It has been relocated numerous times since its initial discovery. Previous placement within section Strigulosi is, however, open to question. More apparently it belongs within the Scytocarpi, near *A. gracilis*.

Astragalus tegetarioides M.E. Jones, Contr. W. Bot. 10:66. 1902. Bastard kentrophyta.

Prostrate, caulescent perennial, forming mats or cushions 1–3 (4) dm wide, radiating from a branching caudex. **Pubescence** strigose or thinly villosulous, basifixed. **Stems** 5–15 cm long or more. **Stipules** 0.8–3 (5) mm long, at least the lower ones connate-sheathing. **Leaves** 1–4 (6) cm long; leaflets (5) 7–11, 1.5–5.5 (7) mm long, obovate-cuneate, obtuse, truncate, or emarginate, pubescent on both sides. **Peduncles** 0.3–2.5 cm long; racemes compactly or loosely (2) 3- to 6 (8)-flowered, the flowers ultimately declined at anthesis, the axis 3–15 mm long in fruit; bracts 1.2–2.7 mm long; pedicels 0.4–1.3 mm long; bracteoles 0. **Calyx** (2.2) 2.6–3.7 mm long, the tube 1.1–2 mm long, obconic-campanulate, the teeth 1–1.9 mm long, subulate. **Flowers** 4.4–6 (7) mm long, whitish, the banner faintly lilac-veined. **Pods** spreading, sessile, the body 3.5–4.5 mm long, 1.5–4.2 mm wide, ovoid-lenticular, obscurely trigonous, minutely strigulose to silky villous. **Ovules** 2–3 (4).

1\. Racemes loosely 2- to 6 (8)-flowered; flowers whitish, the banner with pale lilac veins, 4.4–7 mm long; pods 1.5–2.8 mm wide; plants of Harney Co., Oregon . . . . var. *tegetarioides*

1. Racemes compactly (7) 9- to 15-flowered; flowers rose purple, the banner with a pale basal eye, 6.5–10 (12) mm long; pods 3.2–4.2 mm wide; plants of Lassen Co., California . . . . var. *anxius*

Astragalus tegetarioides var. *tegetarioides*

Pubescence strigose-strigulose. **Leaflets** 7–11, 1.5–5.5 mm long. **Racemes** 1.3–1.8 cm long, loosely 2- to 6 (8)-flowered. **Calyx** (2.2) 2.6–3.7 mm long, the teeth 1–1.9 mm long. **Flowers** 4.4–6 (7) mm long, the banner reflexed 70–100°. **Pods** 3.3–4.5 mm long, 1.5–2.8 mm wide. *Type: "No. 2619 Cusick, southern Blue Mts., Oregon, in sandy soil in the Buck Range, June 28, 1901"; holotype POM!; isotypes G, GH!, K, MO, ND, NY!, ORE, P, RM, US!*

Dry pine forests and sagebrush communities at ca 1350–1550 m in the Little Juniper Mountain and upper Silvies River, in west central and north Harney Co., Oregon.

Astragalus tegetarioides var. *anxius* (Meinke & Kaye) Welsh, comb. nov.

[*A. anxius* Meinke & Kaye, Madroño 39: 194. 1992].

Pubescence loosely villous to pilosulous. **Leaflets** 9–15, 4–9 mm long. **Racemes** 0.8–2.2 cm long, compactly 7- to 13 (15)-flowered. **Calyx** 3.2–4.7 (5) mm long, the teeth 1.7–2.7 mm long. **Flowers** 6.5–10 (12) mm long, the banner reflexed 60–80°. **Pods** 3.5–4.5 mm long, 3.2–4.2 mm wide. *Type: "California, Lassen Co., Ash Valley, ca 25 km west of Madeline and U.S. Hwy. 395, immediately south of Ash Valley Rd., in loose gravel overlying volcanic bedrock, on the boundary of T38N, R11E, Sect. 32 and T37N, R11E, Sect. 5, ca 1550 m, 16 Jul 1991, Meinke and Lantz 6108," holotype OSC; isotypes CAS, ISC, MO, NY, RM, UC, US.*

Arid flats in or near juniper-sagebrush steppe or *Pinus jeffreyi* woods at 1540–1660 m, in Ash Valley, extreme north central Lassen Co., California.

Astragalus ampullarioides (Welsh) Welsh comb. nov. Shivwits milkvetch.

[*A. eremiticus* var. *ampullarioides* Welsh, Great Basin Naturalist 46:262. 1986].

Moderate, caulescent perennial, 20–63 cm tall, from a branching subterranean caudex. **Pubescence** thinly strigulose, basifixed. **Stems** decumbent to erect, buried for a space of 2–10 cm. **Stipules** 3–9 mm long, all distinct. **Leaves** 5–22 cm long; leaflets 13–21, 4–24 mm long, 3–17 mm wide, ovate to obovate, lanceolate, or elliptic obtuse to retuse, strigose (along veins) beneath, ciliate, glabrous above. **Peduncles** (4) 9–23 cm long; racemes (15) 20- to 40-flowered, the flowers ascending anthesis, the axis (4) 10–16 cm long in fruit; bracts 1.5–4 mm long; pedicels 0.7–3.5 mm long; bracteoles 0–2. **Calyx** 5–6 mm long, the tube 4–5 mm long, short-cylindric, strigose, the teeth 0.5–0.9 (1.2) mm long, triangular to subulate. **Flowers** (11) 14–18 mm long, ochroleucous, the keel immaculate, the banner recurved through ca 25°. **Pods** erect, slenderly stipitate, the stipe 7–15 mm long, the body ovoid to ellipsoid, inflated, papery, 12–18 mm long, 8–10 (12) mm thick, obcompressed, glabrous, essentially unilocular, the septum to ca 0.2 mm wide. *Type: "Washington Co., Utah . . . ca 1 mi N hwy 91 at Shivwits, 3450 ft. elev. S.L. Welsh, N.D. Atwood 21049, 21 April 1982," holotype BRY!*

Flowering April, May. Gypsiferous substrates, in "boils" on the Chinle Formation surrounded by creosote bush, other warm desert shrubs, and juniper communities at ca 1050–1150 m from the Petrified Forest section of Zion National Park, west in several disjunct populations to the type locality, Washington Co., Utah.

The Shivwits milkvetch was dismissed as taxonomically inconsequential by Barneby (1989) and by Isely (1996). However, the combination of subterranean caudices, fistulose stems, very large number of flowers on an attenuated raceme, and papery inflated pods seems to be a rather consequential grouping of taxonomic features, especially in a plant with a preference for harsh ecological substrates. Diagnostic criteria are of the order of magnitude of those utilized elsewhere to distinguish the closely related *A. ensiformis* M.E. Jones from *A. minthorniae* (Rydberg) Jepson. The nature of the root crown and of the pods, but not of the remainder of the plant, is reminiscent of the only slightly allopatric *A. ampullarius* S. Watson. Plants of the Shivwits milkvetch are routinely hedged back by deer. Often the entire inflorescence is consumed.

Astragalus cutleri (Barneby) Welsh, comb. nov. Cutler's milkvetch.

[*A. preussii* var. *cutleri* Barneby, Great Basin Naturalist 46:256. 1986].

Moderate, caulescent, short-lived perennial, often flowering as an annual, 10–30 (35) cm tall, from a superficial caudex. **Pubescence** sparingly strigulose to subglabrous, basifixed. **Stems** few to several, ascending to erect, forming bushy clumps. **Stipules** 2–6.5 mm long, all distinct. **Leaves** 3–13 cm long; leaflets 5–17 (19), 3–17 (20) mm long, (3) 5–12 mm broad, elliptic to lanceolate, oblanceolate or obovate, acute to obtuse or mucronulate, strigulose to glabrous below, glabrous above. **Peduncles** 2.5–10 cm long; bracts 1.5–2.5 mm long; racemes 5- to 9-flowered; pedicels 1.5–2.5 mm long; bracteoles 2. **Calyx** (7.3) 7.5–8.5 (9) mm long, the tube 5.9–6.7 long, cylindric, pale purple or whitish, sparsely black-strigose, the teeth 1.3–1.7 (2.3) mm long, subulate. **Flowers** 15–16 mm long, white or tinged (or drying) purplish, the banner recurved through ca 40–45°. **Pods** ascending to erect, stipitate, the stipe 3–3.5 mm long, the inflated body oblong-ellipsoid, 14–18 mm long, 9–11 mm thick, the valves thinly cartilaginous, greenish suffused (sometimes) with purple, unilocular, glabrous. **Ovules** 20–38. *Type: "Cutler 2283, Copper Canyon, 1 mi from mouth, San Juan Co., Utah," holotype NY!, isotypes CAS!, WIS.*

Flowering April, May. Saltbush and blackbrush communities, on Permian formations, at ca 1155–1250 m, at Copper Canyon south of San Juan Arm of Lake Powell, San Juan Co., Utah.

This taxon, when first characterized, was known only from plants flowering as annuals. Later collections demonstrate that the plant is at least a short-lived perennial. The other characters hold, however, even if there is more overlap in leaflet number than previously known. Also, the pods are of thin texture, approaching *A. eastwoodiae* more so than *A. preussii*, with which it shares features of ascending-erect pods. Cutler's milkvetch differs from *A. preussii* in about the same order of magnitude as does *A. eastwoodiae*.

***Astragalus sabulosus* M.E. Jones, Zoë 2: 239. 1891. Cisco milkvetch.**

Robust, ill-scented, caulescent perennial, 13–38 cm tall, from a woody superficial caudex. **Pubescence** strigulose, basifixed. **Stems** decumbent to ascending or erect, several to numerous, forming clumps. **Stipules** 4–9 mm long, all distinct. **Leaves** 3–10.5 cm long; leaflets 5–11, 6–35 (50) mm long, 3–17 mm wide, rhombic-oval to obovate or elliptic, mucronate, strigose to glabrous on both sides. **Peduncles** 3.5–7 cm long; racemes 4- to 10-flowered, the flowers ascending-spreading at anthesis, the axis 0.5–2 cm long in fruit; bracts 2–6 mm long; pedicels 2–5 mm long; bracteoles 0–2. **Calyx** 15–17.5 mm long, the tube 11.5–14 mm long, cylindric, strigulose, the teeth 3–4 mm long, subulate. **Flowers** (23) 27–34 mm long, ochroleucous, fading yellowish or white fading off-white. **Pods** spreading to declined, subsessile, inflated, cylindroid, 20–48 mm long, 10–15 mm thick, stiffly papery to leathery, strigose, unilocular. **Ovules** 55–59; 2n = 26.

1. Flowers 27–34 mm long, ochroleucous, fading yellowish; plants of the Cisco-Thompson vicinity . . . . var. *sabulosus*
1. Flowers 23–27 mm long, white, fading off-white; plants from northwest of Moab . . . . var. *vehiculus*

Astragalus sabulosus* var. *sabulosus

[*Jonesiella sabulosa* (M.E. Jones) Rydberg].

Calyx 15–17.5 mm long, the tube 11.5–14 mm long, cylindric, strigulose, the teeth 3–4 mm long, subulate. **Flowers** 27–34 mm long, ochroleucous, fading yellowish. **Pods** spreading to declined, subsessile, inflated, cylindroid, 20–48 mm long, 10–15 mm thick, leathery. *Type: "Collected [by M.E. Jones] May 2, 1890, at Cisco, Utah, on gravelly soil near Grand River"; holotype POM!*

Flowering late March to May. Mat-atriplex-shadscale communities at 1300–1600 m on Mancos Shale (and Morrison Formation?) in the Grand River Valley, vicinity of Thompson and Cisco, Grand Co., Utah.

The very large, pale ochroleucous flowers are borne in late March through April and by mid-May the plants bear large sausagelike fruits. The Cisco milkvetch is a primary selenium indicator with close affinities to both var. *vehiculus* and *A. iselyi* Welsh (q.v.), from both of which it can be distinguished by its ochroleucous flowers that fade yellow (Welsh 1994). The flowers of *A. sabulosus* var. *sabulosus* are the largest within *Astragalus* in Utah, and possibly elsewhere (though they are not the longest). Understanding of diversity within the *sabulosus* complex was long held in abeyance because of paucity of flowering specimens in herbaria. Those that were collected were taken in fruiting condition. Floral features readily allow segregation of the known populations into 3 taxa, *A. isely*, *A. sabulosus* var. *sabulosus*, and *A. sabulosus* var. *vehiculus*.

***Astragalus sabulosus* var. *vehiculus* Welsh, var. nov.**

Similis var. *sabulosi* sed in floribus minoribus (2–27 nec 27–34 mm) et albidis (nec ochroleucis) decolore albidis (nec flavis) et leguminibus substipitatis incipientibus. *Type: Utah, Grand Co., T24S, R20E, Sec 7, ca 16 mi due NW of Moab, ca 4500 ft. elev. Morrison Formation, mixed salt desert shrub comm., 28 Apr 1984, S.L. Welsh 22709, holotype BRY!, 3 isotypes distributed previously as *Astragalus sabulosus*.* Additional specimens (all BRY!): Utah, Grand Co., ca 1 km SSE of historic state station and 20 km NW of Moab, at ca 1464 m elev., 30 April 1984, S.L. Welsh & D. Trotter 22723 (fl.); do, 20 May 1985, S.L. Welsh 23432 (fr.); do, 21 May 1984, Atwood, Goodrich, and Thompson 9700; do, T24S, R20E, S16 SESW, ca 1.8 miles N of Courthouse Rock, 16 June 1995, D. Atwood 20276.

Calyx 12–16 mm long, the tube 11–13 mm long, cylindric, black strigulose, the teeth 2–3.5 mm long, subulate. **Flowers** 23–27 mm long, white, fading whitish. **Pods** spreading to declined, subsessile to incipiently substipitate, inflated, cylindroid, 28–45 mm long, 9–13 mm thick, stiffly leathery,

Shadscale, woody-aster, galleta community on the Morrison Formation at 1370–1465 m near the head of Courthouse Wash, Grand Co., Utah.

Plants of var. *vehiculus*, the stage station milkvetch, approach *A. iselyi* in flower color but have much larger flowers. They are geographically disjunct, by more than 35 km from *A. iselyi* and about that distance from the nearest known population of var. *sabulosus*. The *sabulosus* complex is also allied with *A. praelongus* Sheldon, which has much smaller flowers and pods.

***Astragalus laccoliticus* (M.E. Jones) Welsh, comb. nov. Laccolite milkvetch.**

[*A. cicadae* var. *laccoliticus* M.E. Jones, Proc. Calif. Acad. Sci. II. 5:672. 1895].

Perennial, acaulescent, 4–8 cm tall, from a taproot and superficial caudex. **Pubescence** dolabriform. **Stems** obsolete or essentially so, the internodes obscured by stipules. **Stipules** 2–5 mm long, all distinct. **Leaves** 2–9 cm long; leaflets (5) 9–11, (4.5) 5–11 mm long, 3.5–6.5 mm wide, oblanceolate to obovate, obtuse, strigose on both sides. **Peduncles** 1.3–6 cm long; racemes 3- to 8-flowered, the flowers spreading-ascending, the axis 3–15 cm long in fruit; bracts 2–5 mm long; pedicels 1–2.5 mm long. **Calyx** 10–11.5 mm long, the tube 8.5–10 mm long, cylindric, strigulose, the teeth 1–2 mm long. **Flowers** 19–27 mm long, pink-purple, fading or drying ochroleucous. **Pods** ascending (humistrate), sessile, the body 15–25 (27) mm long, 7–15 mm thick (when pressed), turgidly lance-ovoid, contracted distally into an incurved, laterally compressed beak 5–8 mm long, fleshy, the valves ca 2 mm thick, shrinking in ripening, green or purplish, but not mottled, strigulose, unilocular. **Ovules** ca 38. *Type: M.E. Jones, "No. 56581. July 21, 1894, at Cottrell's Ranch, Henry Mountains, Utah, 6000° alt.," holotype POM!*

Salt desert shrub, Bigelow sagebrush, and juniper communities, at 1460–1890 m, in western Wayne and western Garfield counties (Henry Mts. and vicinity), Utah.

The laccolite milkvetch is easily distinguished from *A. chamaeleuce* A. Gray by its lance-ovoid (not ellipsoid, purple-mottled pods). The taxon has been confused with the nearby *A. consobrinus* (Barneby) Welsh, with which it shares structurally similar but much larger pods and flowers, and has been treated previously as a variety of *A. chamaeleuce*, whose distribution is adjacent to but not confluent with that of this plant. Its morphological differences are similar to those regarded as diagnostic in other taxa within the Argophylli.

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REGIONAL ASSESSMENT OF WADABLE STREAMS IN IDAHO, USA

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ABSTRACT.—There has been a resurgence in applying bioassessment techniques for evaluating and monitoring the biological integrity of stream ecosystems. In all cases biological metrics have been refined to account for regional variation in aquatic habitats and fauna. This study evaluated environmental and macroinvertebrate properties for wadable streams in 3 major ecoregions of Idaho: Northern Basin and Range, Snake River Plain, and Northern Rocky Mountain. These 3 ecoregions constitute >80% of the land area in Idaho. Reference streams were delineated from test streams in each ecoregion using standard habitat assessment protocols (Plafkin et al. 1989). Multiple discriminant analysis effectively determined habitat (quantified measures) and macroinvertebrate differences between reference and test streams within ecoregions, although the results suggested that quantifiable habitat measures (e.g., water chemistry and nutrients) and biotic metrics based on taxonomic groups (e.g., % Elmidae) improved the discriminatory power of evaluation procedures. Our results support the contention of a multi-metric approach for assessing differences among streams within an ecoregion. Lastly, individual metrics differed in their importance for evaluating stream condition among ecoregions, further emphasizing the importance of regionally stratifying metric selection or scoring procedures.

Key words: bioassessment, ecoregion, habitat, Idaho, macroinvertebrates, phosphorus.

Although the Clean Water Act directs the U.S. Environmental Protection Agency to develop programs to evaluate, restore, and maintain the integrity of its waters, freshwater lakes and streams continue to be seriously degraded by nonpoint source pollutants and habitat alterations associated with various land-use practices (Benke 1990, Hughes et al. 1990, Karr 1991, Hughes and Noss 1992, Allan and Flecker 1993, Richards et al. 1993, 1996). Historically, water quality assessment focused primarily on chemical criteria and single-factor laboratory toxicity tests. The nature of nonpoint source pollution (e.g., sedimentation) and related changes in physical habitat, however, requires alternative methods for assessing the biotic "health" of freshwater systems (Minshall 1996). Presently, many states have implemented an ecoregion approach in their bioassessment programs (e.g., Fausch et al. 1984, Gallant et al. 1989, Southerland and Stribling 1995, Barbour et al. 1996). An ecoregion (areas of similar geography, hydrology, climate, chemistry, terrestrial vegetation, and biota) approach was adopted to account for geographical differences (variability) in freshwater habitats and fauna, and the differential response of respective regions to anthropogenic impacts (Bailey 1989, Gallant et al. 1989, Hughes et al. 1990, Matthews et al. 1992).

Rapid bioassessment protocols have become an important tool in the biological evaluation of stream ecosystems (Karr et al. 1986, Plafkin et al. 1989, Karr 1991). These protocols are based on a strong theoretical framework in community and ecosystem ecology, although specific metrics usually are modified to adjust nationally derived or general criteria to meet regional conditions (Steedman 1988, Barbour et al. 1992, Resh and McElravy 1993, Barbour et al. 1996). Rapid bioassessment protocols were developed originally for the time- and cost-effective collection of biological data, although compromising data completeness (e.g., qualitative sampling techniques) and reliability (e.g., no measure of data variability resulting in a loss of statistical power and potential for Type II errors; Resh and Jackson 1993). More specifically, rapid bioassessment attempts to use regional biota to determine water and habitat quality, and thus evaluate stream ecosystem integrity and health (Rosenberg and Resh 1993, Barbour et al. 1996). For example, protocols have been developed using fish, macroinvertebrates, and algae to provide a more integrative ecosystem-level assessment of biological integrity

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(Bramblett and Fausch 1991, Barbour et al. 1992, Reice and Wohlenberg 1993). Idaho recently issued a number of monitoring protocols that use fish (Chandler and Maret 1993) or macroinvertebrates (Clark and Maret 1993) in conjunction with habitat evaluation guidelines (Burton 1991, Burton et al. 1991) for assessing the biological integrity of its streams.

The present study incorporated rapid bioassessment protocols for assessing the biological conditions of wadable streams in the Northern Basin and Range (NBR), Snake River Plain (SRP), and Northern Rocky Mountain (NRM) ecoregions within Idaho. We examined a variety of habitat and biotic measures used for assessing the biological integrity of lotic systems and evaluated their respective applicability to conditions found in these 3 ecoregions. We focused our work on the NBR and SRP ecoregions in the southern part of the state in 1990 and 1991, and included the NRM ecoregion in 1993 (Robinson and Minshall 1995a). These 3 ecoregions constitute >80% of the land area in Idaho. We examined the responsiveness of measures among streams that differed in the degree of impact by land uses characteristic of the particular region. Undisturbed or "least" impacted streams, which serve as the reference condition for determining degree of degradation of test streams, thus provide the foundation for developing predictive models (generalizations) regarding stream integrity in a particular area or ecoregion in Idaho.

METHODS

Selection of Study Sites

We selected study sites from candidate streams by reviewing existing literature concerning site conditions, by discussing options with various agency personnel (Bureau of Land Management, Idaho Division of Environmental Quality, Idaho Department of Fish and Game, and United States Forest Service) and private landowners, and by field reconnaissance. Where possible, we made special effort to select designated "stream segments of concern" (Clark 1990, Dunn 1990). Site locations range from the Idaho/Wyoming border to the Idaho/Oregon border; many sites are accessible only via a dirt track or by foot. Eighty-five 2nd- to 4th-order streams (after Strahler 1957) were selected for analysis and included reference (r) and test (t) sites in each ecoregion (NBR: r = 14, t = 18; SPR: r = 16, t = 12; NRM: r = 16, t = 9). Test sites in the NBR and SRP ecoregions are usually lowland areas perturbed primarily by livestock grazing and other nonpoint source agricultural inputs. Mining is the major land use in the NRM. A complete list of study streams and specific locations can be found in Robinson and Minshall (1995a).

Collection Procedures for Physical and Chemical Measures

Initially, we evaluated habitats using qualitative habitat assessment procedures as defined in Plafkin et al. (1989). Streams with summed habitat assessment values ≥80% of the possible maximum score were used as reference streams; those with lower scores were considered test streams. In addition, other habitat measures were quantified at each site. Specifically, we calculated average bank-full widths at each study site from 5 transects 50 m equidistant. We estimated canopy cover for the entire reach (ca 250 m) and presented it as quartile percent, i.e., 0, 25, 50, 75, or 100% coverage. Substratum size (x-axis), embeddedness (quarter system as for % canopy cover) values, and water depth were measured from 100 randomly chosen stones (locations for depth) within a 100-m section of each study reach. Using an Orion (model 126) conductivity meter standardized to 20°C, we measured specific conductance in the field. Field pH was measured with either an Orion (model SA250) or Schott (model CG 837) pH meter. Alkalinity and hardness were quantified in the laboratory using standard methods (APHA 1992). Nitrate and phosphorus concentrations were measured using a HACH meter (model DR2000) and HACH reagents. Water velocities for calculations of discharge were determined using an Ott C-1 meter.

We collected periphyton by scraping all material from a known area on the surface of 5 stones and transferring the material onto separate Whatman GF/F glass-fiber filters (*n* = 5/site; after Robinson and Minshall 1986). Upon filtering, the material was kept frozen at –25°C until analysis in the laboratory for chlorophyll a and AFDM. Initially, we ground samples in reagent-grade acetone using a Brinkmann tissue homogenizer (model PT 10/35). Chlorophyll a was extracted in reagent-grade acetone and quantified using a Gilford Model 2600 spectrophotometer (APHA 1992). Samples from

1993 were extracted in 100% methanol; methanol extraction eliminates the need to grind samples (Holm-Hansen and Riemann 1978). Although both extraction media result in similar extraction efficiencies, we conducted a test to compare chlorophyll a concentrations from samples using both media. Chlorophyll a was extracted from samples in acetone or methanol and quantified as above. The results indicated no difference between the methanol and acetone methods ($p = 0.76$, independent samples t test, $n = 20$). Periphyton AFDM of each sample was determined as described above for BOM (see below) using the remaining material from chlorophyll a analysis.

Depending on the year of study, we used semiquantitative and quantitative collection techniques for sampling macroinvertebrates to meet specific study objectives for that year. In 1990 semiquantitative sampling was conducted at all selected sites, and an additional 5 quantitative samples were collected at 5 of these sites. In 1991 and 1993 we completed quantitative sampling at all selected sites, with additional semiquantitative samples collected at 10 of these sites in 1991. Benthic macroinvertebrates were semiquantitatively collected from riffle/run habitats using a metal-framed net (1-mm mesh in 1990 and 500-μm mesh in 1991 and 1993, 30 cm high × 60 m wide × 100 cm long) affixed to a D-style shovel handle. A 3-min sample was proportioned among riffle and run habitats along a 150-m length of stream and preserved in the field with 10% formalin (Plafkin et al. 1989; also see Resh and Jackson 1993). Using a modified Hess net (250-μm mesh), we collected quantitative benthic samples at 5 riffle/run habitats at each site. Although different mesh sizes were used between years, no statistical differences were found between respective biotic metrics at a particular site (Robinson and Minshall 1995a).

Benthic organic matter was estimated from material obtained in the quantitative macroinvertebrate samples. Following removal of macroinvertebrates, organic matter was determined by drying the sample at 60°C for at least 48 h, weighing, ashing at 550°C for 2 h, rehydrating, redrying for at least 24 h, and reweighing. The difference in dry weights was the quantity of organic matter (as AFDM) for that sample. In the laboratory we systematically hand-picked a 300-count sample of macroinvertebrates from each semiquantitative sample for metric analysis. In 1990 all macroinvertebrates were removed from each quantitative sample. In 1991 and 1993 the 5 quantitative samples from a site were combined and, following the initial removal of large and rare taxa, a minimum of 300 organisms were systematically hand-picked from the combined sample (analogous to the 2-phase sample processing described by Cuffney et al. 1993; also see Courtemanch 1996). We identified all picked macroinvertebrates to lowest feasible taxonomic unit (usually genus) and enumerated them.

Biotic metrics were calculated from the macroinvertebrate data from each site as described in Winget and Magnum (1979), Platts et al. (1983), Fisher (1989), Plafkin et al. (1989), Chandler and Maret (1993), and Clark and Maret (1993). Seventeen metrics were calculated for benthic macroinvertebrates: ratio of Ephemeroptera, Plecoptera, and Trichoptera (EPT) abundance to Chironomidae (CH) and Oligochaeta (O) abundance (EPT/CH+O); species richness; EPT richness; Hilsenhoff Biotic Index (HBI); Biotic Condition Index (BCI); ratio of EPT/CH; % dominant taxon; Shannon's diversity index (H'); Simpson's dominance index (C); ratio of shredders to total macroinvertebrate abundance; macroinvertebrate density; % scrapers; % filterers; % shredders; % EPT taxa; % CH+O; and % Chironomidae. The HBI used an assigned scale of 0–10 (Hilsenhoff 1988) and regional tolerance values from Clark and Maret (1993).

For the 25 sites evaluated in 1993 in the NRM, we calculated macroinvertebrate metrics from Fisher's (1989) data due to budget limitations. Fisher (1989) assessed 137 sites in the NRM, data which the State of Idaho wanted to incorporate into their biomonitoring program. For quality assurance, we collected macroinvertebrates from 4 of these sites and compared biotic metrics for macroinvertebrates with respective data from Fisher (1989). Although some discrepancy existed in identification of taxa (Fisher consistently had higher species richness and EPT richness values), most other biotic metrics appeared robust enough to mitigate the differences. For example, highly similar values were found for % EPT and % CH+O. Based on these results, we felt confident that metrics could be calculated for all 25 streams using Fisher's data in concert with our habitat measures. To eliminate discrepancies in richness values, we combined some obvious "split" taxonomic groups, e.g., *Baetis* species. Specimens of all macroinvertebrate taxa collected during the study were retained for voucher collections and housed at the Stream Ecology Center of Idaho State University, Pocatello; Idaho Department of Health and Welfare, Bureau of Laboratories, Boise; and Orma J. Smith Museum of Natural History, Albertson College of Idaho, Caldwell.

We completed separate multiple discriminant analyses (MDA) using quantitative habitat measures, biotic metrics, and relative abundances of the most common taxa or taxonomic groups to determine variables that best differentiated reference and test streams in each ecoregion (Tabachnick and Fidell 1989). Some taxa were combined at the generic (e.g., *Ephemerella*) or family (e.g., Elmidae) level to provide enough data for statistical comparisons; all combined taxa had equal tolerance values (after Clark and Maret 1993). These taxonomic groups generally comprised over 80% of the macroinvertebrate assemblage at any one site. One-way ANOVA was used to determine differences in quantified habitat variables of reference streams among ecoregions; variables were transformed prior to analysis to improve data homoscedasticity (Zar 1984). Following MDA, we scored selected biotic metrics for each ecoregion similarly to methods described in Barbour et al. (1996). Briefly, metrics that had values greater or lesser (i.e., dependent on particular metric) than the median value of reference streams scored 5, those between the 25%ile (or 75%ile) and the median scored 3, and those higher than the 75%ile or lower than the 25%ile scored 1. We then summed individual metric scores for each site to provide an overall score for that stream. Separate *t* tests were performed to test for differences between average reference and test site scores within each ecoregion (Zar 1984).

RESULTS

Habitat Assessment and Environmental Conditions

As designed, reference streams had higher average habitat assessment values (after Plafkin et al. 1989) than test streams in each ecoregion (Fig. 1). Indeed, reference sites had average values 60 points greater than test sites in the NBR and SRP, and 30 points more in the NRM. However, NBR and SRP test streams displayed a wide variation in habitat assessment values that ranged from <30 to 143 (144 was the separation value for reference and test streams). Because of design constraints (see Methods), test streams in the NRM showed much less variation and had higher average habitat scores than test streams in NBR and SRP ecoregions.

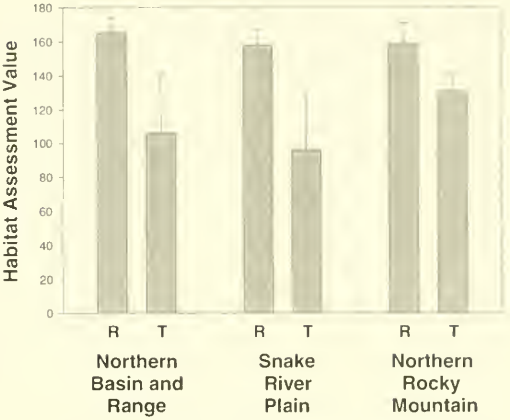

Fig. 1. Average (+1*s*) habitat assessment values (after Plafkin et al. 1989) for reference and test streams within each ecoregion.

Multiple discriminant analysis using quantified habitat measures clearly separated reference streams in each ecoregion (Fig. 2). Reference streams in the NRM were distinguished from other reference streams by lower elevations and lower water temperatures (Root-1), whereas reference streams in the NBR and SRP had similar elevations and temperatures but differed significantly in water chemistry and width:depth ratio (Root-2). Here, reference streams in the NBR had higher ionic measures (e.g., specific conductance, alkalinity, and hardness) and greater depths (i.e., differences in width:depth ratios due to differences in depth not width) than streams in the SRP (Table 1).

There were some major differences in habitat characteristics between reference and test streams within each ecoregion; these differences were especially evident in the NBR and SRP. Physically, test streams typically had lower gradients, more open canopies, smaller substrata, higher substrata embeddedness, and higher water temperatures than reference streams (Table 1). Chemical differences among

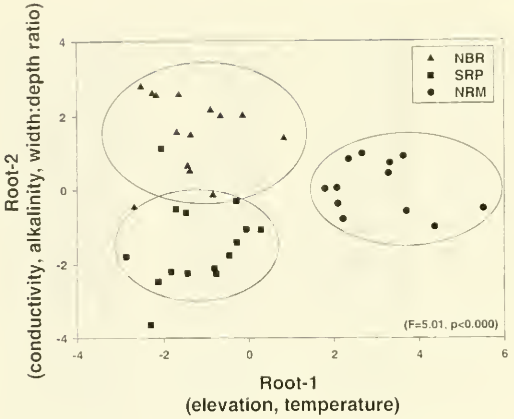

Fig. 2. Multiple discriminant analysis scatterplot of root scores for individual reference streams within each ecoregion based on quantitative habitat measures. Circles independently drawn to illustrate differences among ecoregions.

stream types were most evident in the NBR, with test streams showing 2× higher ion concentrations than reference streams. In addition, phosphorus concentrations were ca 2× greater in test streams than in reference streams, although they were more pronounced in the SRP ecoregion. Again, few differences were observed in habitat conditions between test and reference streams of the NRM, although test streams did display higher water temperatures than reference streams (Table 1). Differences in biotic resources were less evident among test and reference streams due to high variability (e.g., all CVs > 100%). However, there were some trends of enhanced periphyton standing crops in test streams relative to reference streams. For example, average chlorophyll a levels were 4× greater in test streams than in reference streams in the NBR, and periphyton AFDM values were 3× greater in test streams than in reference streams in the SRP. These patterns are contrary to those in the NRM and may reflect a reduction in bryophytes (not quantified in this study) in test streams in this ecoregion (C.T. Robinson personal observation).

Macroinvertebrate Assessment

Multiple discriminant analysis (MDA) revealed important but different metrics for distinguishing between reference and test streams within each ecoregion (Table 2). For example, only EPT richness was an important discriminator between stream types in all ecoregions. Metrics found important for distinguishing stream types in the NBR included EPT richness, EPT/Chironomidae ratio, % Hydropsychidae, % scrapers, % EPT taxa, % CH+O, and % Chironomidae. Important metrics for the SRP included taxa richness, EPT richness, HBI, EPT/CH+O ratio, % dominant taxon, % filterers, and % EPT taxa. Thirteen of 17 metrics were deemed important in the NRM (Table 2), but this high number probably reflected the less degraded conditions of test sites in this ecoregion. MDA results (i.e., root scores for individual sites within each ecoregion) are shown in Figure 3. This type of presentation simply demonstrates that (1) most reference sites were biologically different from test sites (outliers also were evident), and (2) variation in biotic metrics occurred among streams.

MDA based on individual taxa indicated that different taxonomic groups, except the Elmidae, were important for distinguishing among stream types in each ecoregion. Four taxa differentiated reference and test sites in the NBR: Elmidae, Heptageniidae, *Zapada*, and Ephemerellidae (Table 2). For the SRP, these taxa included the Elmidae, Rhyacophilidae, *Brachycentrus*, Capniidae, *Drunella*, Turbellaria, and Simuliidae, whereas *Baetis*, Elmidae, *Zapada*, *Brachycentrus*, *Drunella*, and Simuliidae were important discriminators in the NRM ecoregion. The graphical presentation of site MDA root scores shows clear separation between reference and test streams but, as with the biotic metrics, a high variation in taxonomic properties among study sites within each ecoregion (Fig. 4).

Correlation analysis was used to reveal redundant metrics or taxonomic groups from the MDA results. Of these metrics and taxa, those having the least amount of overlap between reference and test sites were retained for development of a biotic assessment score. Two metrics and no taxa were eliminated from the NRB: EPT/Chironomidae ratio and % CH+O (Table 2). Only taxa richness and *Drunella* were omitted in the SRP, whereas taxa richness, EPT/CH+O ratio, % dominant taxon, Shannon's index, % CH+O, and % Chironomidae were removed from score development in the NRM (no taxa were eliminated in the NRM). Lower, albeit nonsignificant, biotic metric and taxonomic scores were found for test sites relative to reference sites in the NBR (metric, $p < 0.15$; taxa, $p < .15$) and SRP

TABLE 1. Physical, chemical, and resource characteristics for reference (R) and test (T) streams evaluated in each ecoregion. Characteristics expressed as means, standard deviations (Std), and coefficients of variation (CV). Blank cells were sites in which that variable was not recorded. Variables that are underlined showed significant differences between reference and test streams in the NBR or SRP.

		Northern Basin and Range			Snake River Plain			Northern Rocky Mountains		
		Mean	Std	CV	Mean	Std	CV	Mean	Std	CV
PHYSICAL										
Elevation (m)	R	1756	135	8	1630	612	38	1131	298	26
	T	1769	228	13	1586	355	22	1329	409	31
Slope (%)	R	4.1	3.3	80	3.7	3.5	94	3.3	1.4	43
	T	1.6	1.0	65	1.8	1.2	71	2.3	1.4	63
Discharge (m^3/s)	R	0.15	0.64	141	0.12	0.08	67	0.23	0.17	75
	T	0.30	0.33	111	0.23	0.25	144	0.29	0.20	71
Temperature (C)	R	11.2	3.3	29	12.6	4.0	32	7.5	2.6	35
	T	15.1	3.3	22	15.7	4.2	27	9.7	2.6	27
Width (m)	R	3.8	1.2	32	3.4	1.4	43	6.0	2.4	39
	T	3.5	2.0	56	5.1	2.4	48	6.3	3.0	47
Width/depth ratio	R	18.6	8.1	44	21.1	7.5	36	33.9	14.2	42
	T	16.3	7.1	43	25.6	8.5	33	25.7	13.9	54
Canopy cover (%)	R	46	26	56	67	20	30	40	31	76
	T	16	22	137	28	33	118	39	32	82
Substrata size (cm)	R	15.0	7.2	48	15.8	4.9	31	31.6	13.9	44
	T	7.3	6.5	88	9.4	5.2	55	31.2	11.7	37
Embeddedness (%)	R	34	6	19	27	12	45	25	11	43
	T	51	14	28	42	21	51	22	6	29
CHEMICAL										
Specific conductance (umhos)	R	131	112	85	114	56	49	70	40	58
	T	288	146	50	117	66	57	58	22	38
Alkalinity (mg/L $CaCO_3$)	R	62	53	86	45	27	60	41	19	46
	T	138	59	43	59	25	43	36	16	45
Hardness (mg/L $CaCO_3$)	R	88	57	65	48	30	63			
	T	190	61	32	66	32	49			
pH	R	8.2	0.4	5	8.2	0.4	5	8.0	0.4	5
	T	8.4	0.2	3	7.8	0.6	8	7.7	0.1	1
Nitrate (mg/L NO_3)	R	0.09	0.06	69	0.07	0.03	48			
	T	0.07	0.03	49	0.08	0.06	75			
Phosphorus (mg/L PO_4)	R	0.06	0.04	57	0.13	0.13	101			
	T	0.10	0.11	106	0.26	0.23	86			
BIOTIC RESOURCES										
Benthic organic matter (g/m^2)	R	127.2	240.1	189	22.9	19.4	85			
	T	76.8	95.1	124	46.5	82.8	178			
Periphyton chlorophyll a (mg/cm^2)	R	7.1	8.5	120	15.6	17.7	113	45.3	47.3	104
	T	28.3	64.7	229	18.1	23.8	131	22.8	13.8	61
Periphyton AFDM (mg/cm^2)	R	24.1	43.5	181	12.6	27.8	221	66.9	41.2	62
	T	10.1	10.9	108	39.1	86.1	220	72.4	24.5	34

(metric, $p < 0.10$; taxa, $p < 0.13$) ecoregions, whereas respective metric scores were essentially identical in the NRM (metric, $p < 0.51$; taxa, $p < .79$; Fig. 5). However, combining scores from metrics and taxa caused reference sites to have significantly greater average scores than test sites in the NBR ($p < 0.02$ with 2 outliers removed) and the SRP ($p < 0.01$), indicating inclusion of taxonomic metrics provided additional important biotic information on stream condition. The 2 outliers in the NBR actually had habitat assessment scores of 142 and 143, very close to the arbitrary separation score of >144 for reference streams, suggesting this biotic scoring technique is robust for assessing stream condition.

DISCUSSION

The primary goal of the study was to examine a series of abiotic and biotic metrics for assessing biological integrity in 2nd- to 4th-order streams within the NBR, SRP, and NRM ecoregions of Idaho. Collecting these baseline data from reference or "best case" streams and degraded systems allows the development of biological criteria for each ecoregion for use by resource managers. In general, the same

TABLE 2. MDA factor coefficients for metrics and taxa found significant for discriminating between reference and test sites within each ecoregion. Separate analyses were completed for metrics and specific taxa within each ecoregion. Values in bold indicate redundant metrics omitted from score development for that ecoregion (see Methods).

Metric variable	Northern Basin and Range	Snake River Plain	Northern Rocky Mountains
Taxa richness		**–1.13**	**0.45**
EPT richness	1.39	2.41	–2.37
HBI		–0.37	–3.59
BCI			
EPT/Chironomidae	**–1.47**		–2.31
EPT/Chironomidae+ Oligochaeta		1.37	**1.07**
% dominant taxa		–0.78	–0.86
% Hydropsychidae	0.82		2.24
Shannon's			**4.78**
Simpson's			5.56
% scrapers	1.77		1.11
% filterers		–1.27	
% shredders			0.78
% EPT taxa	–2.46	–2.78	
% Chironomidae+ Oligochaeta	**–0.36**		**1.56**
% Chironomidae	–0.90		**–0.87**
Taxon variable			
Baetis			–2.42
Elmidae	0.61	1.01	0.49
Heptageniidae	0.91		
Zapada	–0.58		1.86
Rhyacophilidae		1.28	
Brachycentrus		0.48	–0.25
Ephemerellidae	–0.49		
Hexatoma			
Capniidae		–0.30	
Drunella		**–0.81**	1.23
Turbellaria		0.85	
Sialis			
Simulidae		0.75	–1.43

qualitative habitat assessment measures can be used for evaluating habitat quality in each ecoregion. However, additional research is needed to test whether these differences in qualitative measures are associated with landscape-scale changes and nonpoint source pollution in Idaho (see, e.g., Richards et al. 1996).

In contrast, some quantitative variables for assessing aquatic habitats are important for distinguishing among stream types within and among ecoregions. These measures may better reflect gross changes in landscape properties that are not evident in qualitative habitat assessments but more relevant to aquatic biota. For example, measures of maximum water temperature, substrata size, specific conductance, and nutrients provide important additional information to explain differences in habitat conditions among streams within an ecoregion that also are indicative of dominant land uses or nonpoint source pollution. Further, although ionic concentrations tend to be higher in degraded streams, this finding is more evident for streams in the NBR than in the SRP (the range in habitat assessment values is similar in both ecoregions). Mean chlorophyll a values also are 2–4× higher in degraded sites than in reference sites in the NBR and SRP ecoregions, but the high variability among sites lowers the importance of this factor for assessing aquatic habitats. Our results suggest the importance of including additional quantitative measures, water chemistry in particular, in habitat assessment protocols to more fully describe environmental conditions of a stream (Resh et al. 1995). Current technology allows rapid and

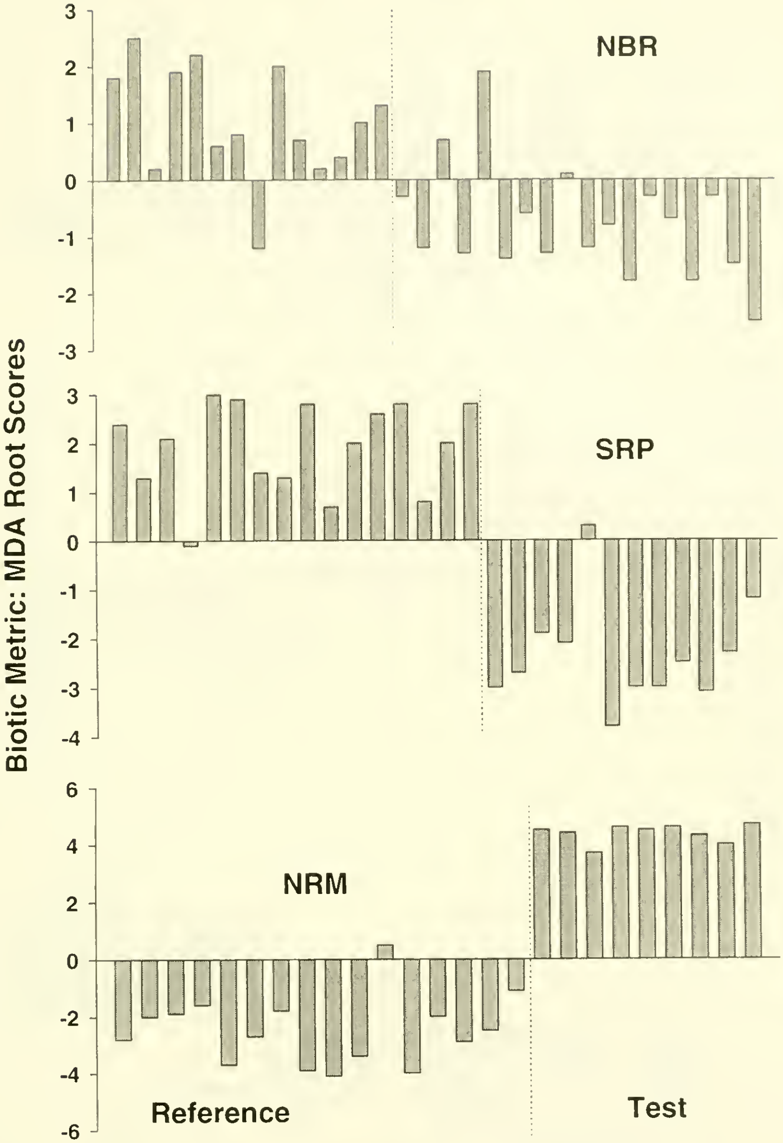

Fig. 3. Histogram of multiple discriminant analysis root scores for individual streams within each ecoregion based on biotic metrics. Dotted line separates reference from test streams. Note the variation among streams within each ecoregion.

accurate field determination of general chemical characteristics and temperature regimes for aquatic systems, which at times can override the importance of other habitat measures in constraining benthic populations.

Macroinvertebrate metrics derived from EPT taxa, measures of dominance, abundances of chironomids, and HBI are important for distinguishing among stream types in each ecoregion. However, the relative importance of some biotic metrics also differs between ecoregions. For example, Chironomidae and Oligochaeta are predominant in the NBR, suggesting that metrics based on these organisms are important for discriminating among stream types in this ecoregion, whereas % filterers is important in the SRP. These findings further demonstrate the necessity of a multi-metric approach to develop and refine biological metrics for specific regions of the country or a state to account

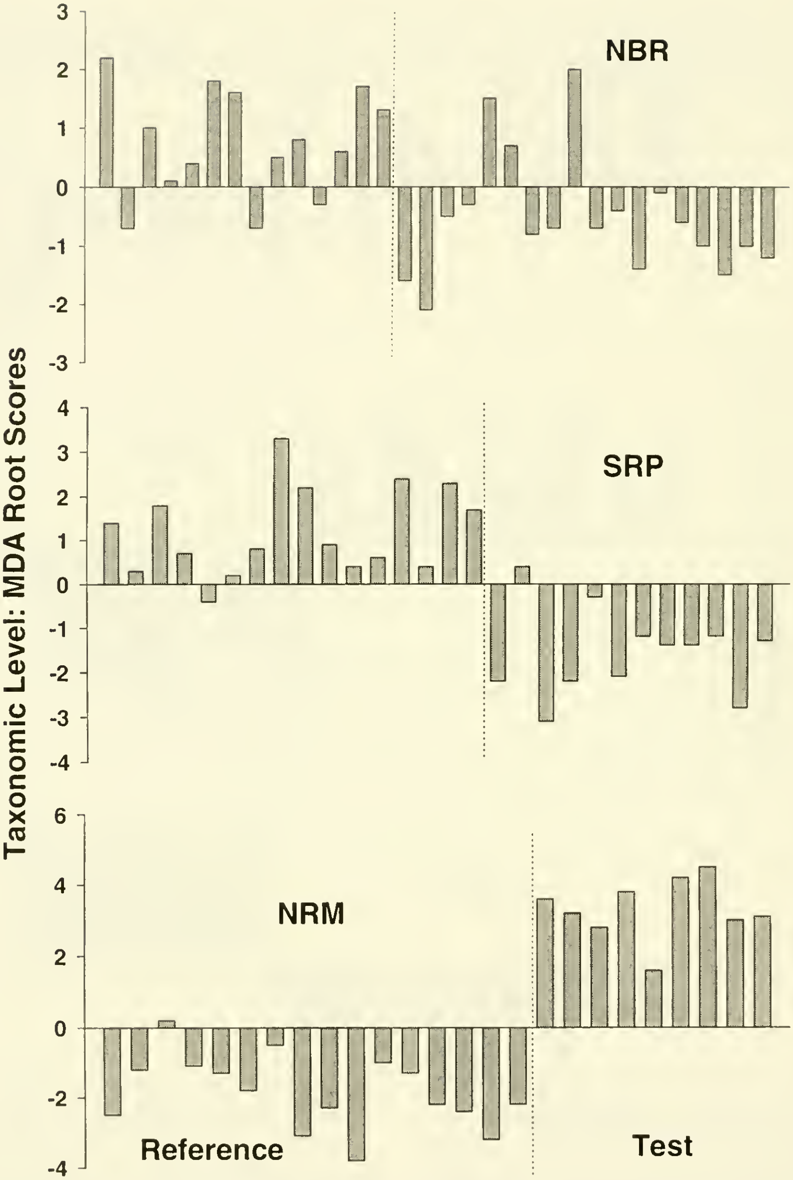

Fig. 4. Histogram of multiple discriminant analysis root scores for individual streams within each ecoregion based on taxonomic groups (see Methods). Dotted line separates reference from test streams. Note the variation among streams within each ecoregion.

for the natural regional variation observed for lotic systems (Hughes et al. 1990). However, readers are directed to Barbour et al. (1996) for an alternative approach that applies a differential scoring regime for using the same biotic metrics among regions.

We examined the potential of additional macroinvertebrate metrics to differentiate stream types by including measures based on the most abundant taxa, excluding chironomids and oligochaetes. Results indicate some taxa, as grouped by family (low abundances precluded use of some individual taxa in multivariate statistics), to be especially sensitive for characterizing stream types (also see Resh and Unzicker 1975, Minshall 1996). For example,

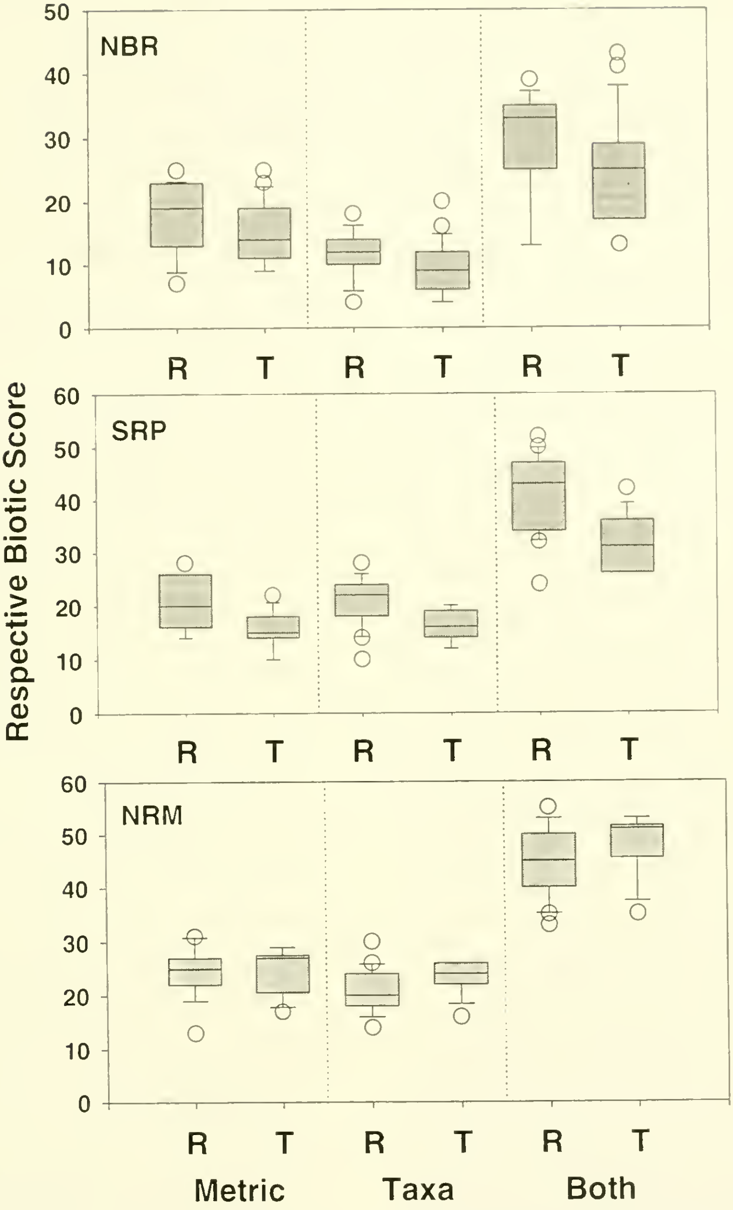

Fig. 5. Box plots for summed metric scores of reference and test streams within each ecoregion for biotic metrics and taxonomic groups separately, and combined metric and taxa scores. Each box plot represents the median, standard deviation, and 90% confidence limits; open circles are outliers.

that some family groups are more abundant in reference (e.g., Elmidae, Heptageniidae, and Rhyacophilidae) than in degraded streams affirms that certain taxa may be especially good indicators of habitat or water quality. Other taxa are abundant enough at the genus level to compare among stream types: *Hexatoma*, *Drunella*, and *Brachycentrus*. The inclusion of taxonomic metrics, whether at the family, genera, or species level, greatly improves the information content and biological relevance of protocols designed to assess lotic integrity (e.g., Robinson and Minshall 1995b).

In summary, different metrics prove important for assessing ecological conditions in streams from different ecoregions in Idaho.

The use of individual metrics also provides important information concerning the kinds of pollution, or changes in the types of pollution or land use, affecting a particular water body. For example, similar types of land use may show different effects on streams among ecoregions because of regional differences in abiotic and biotic properties. Lastly, assessing the biological integrity of streams is complex and requires multiple measures that can elucidate the diverse causes of ecological impairment.

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BATS OF THE WHITE AND INYO MOUNTAINS OF CALIFORNIA–NEVADA

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ABSTRACT.—We surveyed bats throughout the White and Inyo Mountains of California and Nevada. From December 1990 to November 1996, we surveyed hibernating bats, and foraging bats from June 1992 to September 1996. The White–Inyo Range rests in a unique biogeographical junction between the Sierra Nevada, Mojave Desert, and Great Basin regions. Elevational gradients of 305–4340 m, combined with limited human development, further enhance the interest of natural history and faunal distributions in this range. We found 13 bat species in the course of 2668 observations. Three of these species, the spotted bat (*Euderma maculatum*), silver-haired bat (*Lasionycteris noctivagans*), and hoary bat (*Lasiurus cinereus*), have no previous records from the White–Inyo Range. We found bats in all vegetation zones except the alpine, 3500–4342 m. Despite an abundance of mines in this range, only Townsend's big-eared bat (*Corynorhinus townsendii*) and the western small-footed myotis (*Myotis ciliolabrum*) used them routinely. Our data also indicated the importance of surface water to bat populations in arid regions.

Key words: bats, Chiroptera, Great Basin, vegetation zones, habitat, desert, arid regions, water source, hibernation.

The White–Inyo Range rests in the junction of 3 faunal regions: the Sierra Province to the west, Mojave to the south, and Great Basin to the east. Because this range rises abruptly on its east and west sides, animals can readily access a variety of vegetation types over short linear distances. In addition to altitudinal differences, vegetation communities are enhanced by a variety of edaphic sites resulting from the range's high lithographic diversity (Elliot-Fisk 1986). Despite this interesting biogeographical setting, faunal distributions of the range have received little attention. Morrison et al. (1993) provided the first thorough study of bird distributions and habitat use in the White–Inyo Range. However, no systematic survey of bats and their habitat associations in these mountains has been undertaken. Hock (1963) summarized results of a handful of general collecting trips from 1917 to 1958 that yielded some bat specimens. This summary plus an unpublished manuscript from a field course at University of California at Davis (Brosius et al. ca 1974) constitute all prior records.

Our objectives were to provide a detailed account of bat distributions throughout the White–Inyo Range, assess how each species utilizes the different vegetation zones available to it along the range's elevational gradient, and characterize how each bat species uses available mine resources. We report observations from both foraging and hibernating bats. Because the White–Inyo Range remains relatively undisturbed habitat, this baseline may prove useful for tracking long-term alterations in environment, since many researchers consider bats to be sensitive indicators of environmental change (Kunz 1982, McCracken 1986, Thomas 1988). These data also provide useful comparisons for other ranges in the region. Thousands of abandoned mines lie on public and private lands (Shields et al. 1995). The importance of these mines as reservoirs for wildlife displaced from natural habitats has gained increasing recognition (Tuttle and Taylor 1994), and documenting patterns of mine use by bats in the White–Inyo Range may prove useful for present and future management efforts.

STUDY AREA

The White and Inyo Mountains extend for approximately 175 km, forming a contiguous range trending north–south and lying just east of and parallel to the Sierra Nevada. The White Mountains comprise the northern half, located within Inyo and Mono counties, California, and extending into Esmeralda County, Nevada, on their northern reach. The Inyo Mountains extend to the south and lie entirely within Inyo County, California. Elevational gradients span from 300 m at the eastern base of the Inyo Mountains in Saline Valley, California, to the 4342-m summit of White Mountain Peak, California. Annual precipitation varies from less than 10 cm at the base of the range to approximately 50 cm along the northern crest of the White Mountains (Oglesby 1985, Peterson 1986). The Owens and Chalfant valleys (California) form a continuous valley separating the range from the Sierra on the west, while the east side of the range descends into a series of valleys. From north to south they are Fish Lake Valley, located within California and Nevada, and Deep Springs Valley, Eureka Valley, and Saline Valley, all within California. Although we centered this survey on the White–Inyo Range, to fulfill our goal of assessing elevational range we elected to extend our survey of foraging bats into the valley floors at the base of these mountains. Bats foraging in these areas may depend upon rocky outcrops and other features of the mountains for roosts and hibernaculae.

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Five primary vegetation zones occur in the White–Inyo Range along elevational gradients: (1) Mojave mixed desert scrub, characterized by the presence of creosote bush (*Larrea tridentata*), 300–1200 m; (2) Great Basin desert scrub, where shadscale (*Atriplex confertifolia*) is the most common species, 1200–2000 m; (3) pinyon-juniper forest, predominantly singleleaf pinyon (*Pinus monophylla*) interspersed with Utah juniper (*Juniperas osteosperma*), 2000–2900 m; (4) bristlecone–limber pine forest (or subalpine), a mixture of these 2 trees (*Pinus longaeva* and *Pinus flexilis*), 2900–3500 m; and (5) alpine, characterized by the absence of trees, 3500–4342 m.

METHODS

Foraging Bats

We considered bats on the wing from May to October to be foraging. Although active bats are occasionally seen during fair winter weather (Barbour and Davis 1969), these flights may not necessarily be for foraging (Whitaker and Rissler 1989). We surveyed throughout the range in all vegetation zones between June 1992 and September 1996. Although we often could observe bats foraging over open vegetation away from water, we could seldom capture such individuals. Therefore, most of our captures occurred at sources of water that attracted bats (springs, pools, troughs, and stream corridors). We assume these records represent bats observed foraging in the vicinity of those water sources.

Foraging bats were captured over approximately 200 person-days in the field from May through October 1990–1996. We used mist nets or a harp trap set across open flyways near water sources. Four bats recorded in this study were hand-captured from buildings at Deep Springs College, Inyo County, California. We keyed each specimen to species (Ingles 1965, Barbour and Davis 1969, Hall 1981), determined gender (and reproductive status if female), and then released it. We typically maintained the nets from dusk to local 23:30 h depending upon activity, which normally trailed off around 22:30 h. Occasionally, we maintained nets throughout the night but made few additional captures.

Although troublesome to differentiate in other regions, *M. ciliolabrum* and *M. californicus* were readily distinguished in the White–Inyo Range. The White–Inyo *M. ciliolabrum* has a distinctive straw-colored pelage with a highly contrasting dark facial mask and ears. The *M. californicus* we encountered has a chestnut brown pelage with much less contrast to the facial mask and ears (Barbour and Davis 1969, Hall 1981).

We also recorded bats we could identify without capture. In 2 instances, with the aid of binoculars, we identified roosting Brazilian free-tailed bats (*Tadarida brasiliensis*). We then counted individuals as they emerged in the evening. We similarly assessed a colony of pallid bats (*Antrozous pallidus*). The audible calls of the spotted bat (*Euderma maculatum*) enabled species recognition without specialized equipment and supplemented capture records for this species.

Hibernating Bats

We considered inactive bats between the months of November and March to be hibernating. From December 1990 to November 1996, we surveyed 2 natural caves and approximately 260 mines for hibernating bats, working approximately 125 person-days in the field. We entered the mine or cave and visually inspected all accessible reaches, paying particular attention to crevices in the walls and ceilings. We took care to minimize disturbance to bats and other inhabitants by limiting direct light contact and moving quietly through the mine or cave. Species determinations were made by noncontact inspection to avoid disturbance. Fortunately, all species were identified easily in this way. *M. ciliolabrum* was often found 5–10 cm deep in crevices but was recognizable by its size, pointed tragus, straw-colored fur, and almost black facial mask (Barbour and Davis 1969, Hall 1981). Using a mercury field thermometer ±1°C accuracy, we recorded air temperature in the immediate vicinity of roosting bats.

Previous Capture Records

We searched for previous capture records of White–Inyo bats at the Los Angeles County Museum of Natural History (LACM), Museum of Vertebrate Zoology at Berkeley (MVZ), Western Foundation of Vertebrate Zoology (WFVZ), and among the holdings of the University of California White Mountain Research Station. We included these records in our tabulation of observed species and range distributions.

RESULTS

We encountered a total of 13 bat species from 2668 observations during our survey (Table 1). Three species, *E. maculatum*, silver-haired bat (*Lasionycteris noctivagans*), and hoary bat (*Lasiurus cinereus*), were not previously recorded in the White–Inyo Range. The little brown bat (*Myotis lucifugus*) had 1 previous record from this range (LACM); we did not encounter it in our survey (see *Myotis yumanensis* comments in Discussion), although it is known in the nearby Sierra (Hall 1981). *T. brasiliensis*, *E. maculatum*, Townsend's big-eared bat (*Corynorhinus townsendii*), *A. pallidus*, western pipistrelle (*Pipistrellus hesperus*), big brown bat (*Eptesicus fuscus*), long-legged myotis (*Myotis volans*), and western small-footed myotis (*Myotis ciliolabrum*) were all found in both the White and Inyo Mountains portions of the range. *L. noctivagans*, *L. cinereus*, long-eared myotis (*Myotis evotis*), and California myotis (*Myotis californicus*), however, were found only in the White Mountains portion of the combined range. *M. yumanensis* was found only in the Inyo Mountains.

TABLE 1. Compiled observations of bats in the White–Inyo Range, 1990–1997, with previous records shown in parentheses. Previous specimen number for *Myotis volans* is inexact, as it was described as "many" from 3 locations (Museum of Vertebrate Zoology).

Species	Number observed foraging	Number observed hibernating
Tadarida brasiliensis	1185 (5)	—
Euderma maculatum	91*	—
Corynorhinus townsendii	45 (2)	479 (13)
Antrozous pallidus	85 (4)	—
Lasionycteris noctivagans	2	2
Lasiurus cinereus	27	—
Pipistrellus hesperus	410 (18)	4
Eptesicus fuscus	100 (4)	1
Myotis evotis	12 (3)	—
Myotis volans	103 (14+)	1
Myotis californicus	15 (2)	—
Myotis ciliolabrum	33 (4)	49
Myotis lucifugus‡	(1)	—
Myotis yumanensis‡	24 (3)	—
TOTALS	2132 (60+)	536 (13)

*Three captured in mist nets, other records from acoustic detection; see text.
‡We have not listed *M. lucifugus* described by Harris (1974); see text.

We found bats in all vegetation zones except alpine (Fig. 1). The Great Basin desert scrub zone had the highest species richness with 13 species, including the LACM *M. lucifugus* record. Pinyon-juniper was the next richest zone, wherein we recorded 10 species. We recorded 9 species in the Mojave mixed desert scrub zone. We found only 3 species in the bristlecone–limber pine zone; of those 3, only *E. fuscus* and *M. volans* were observed foraging in the zone, whereas *C. townsendii* was recorded hibernating.

The single richest site surveyed was the lower portion of Cottonwood Creek where it enters Fish Lake Valley above the Oasis Ranch on the east side of the White Mountains (T5S R37E, Sec 33; 1600 m elevation). At this site we captured 12 species on separate occasions: *T. brasiliensis*, *E. maculatum*, *C. townsendii*, *A. pallidus*, *L. noctivagans*, *L. cinereus*, *P. hesperus*, *E. fuscus*, *M. volans*, *M. californicus*, *M. ciliolabrum*, and *M. evotis*. The most productive night at this site was 15 August 1995, during which 20 *T. brasiliensis*, 1 *E. maculatum*, 4 *A. pallidus*, 4 *L. cinereus*, 13 *P. hesperus*, 9 *E. fuscus*, 2 *M. volans*, and 1 *M. ciliolabrum* were mist-netted during a 2-h period.

Despite an abundance of carbonate rocks throughout the White–Inyo Range, only 1 cavern is known (2090 m). Located near Westgard

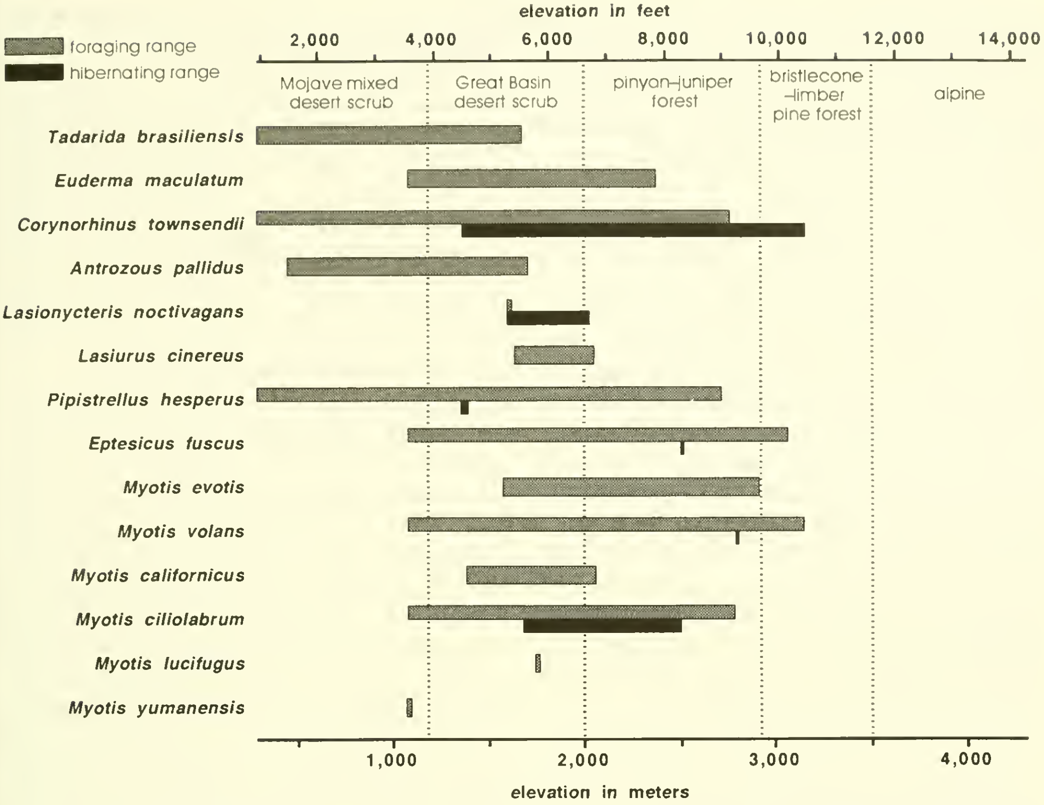

Fig. 1. Elevational distribution of foraging and hibernating bats in the White–Inyo Range showing vegetation zones.

Pass, California, this cavern extends approximately 50 m inward with ceiling heights up to about 25 m. This cavern remains undisturbed because it is protected by a locked gate and remote location and is relatively inaccessible because of its vertical entrance. However, following 4 visits over separate years, we observed only a single *C. townsendii* hibernating within it. A single *C. townsendii* was observed hibernating in a 2-m-deep natural pocket in a dolomite formation in the southern end of the White Mountains (1890 m). On 2 occasions (5 December 1991 and 18 February 1995), an active *L. noctivagans* was found in a dormitory hallway at Deep Springs College. Because of their condition and the dates, we assumed they had been hibernating on the premises. All other hibernation observations were from mines.

We found *C. townsendii* and *M. ciliolabrum* hibernating in mines throughout the range. These species were observed hibernating within about 40 cm of each other. However, we often encountered lone individuals of either species within a mine. We never observed *M. ciliolabrum* hibernating together, but *C. townsendii* were observed in clusters as large as approximately 50 individuals. We observed only 1 individual each of *E. fuscus*, *L. noctivagans*, and *M. volans* hibernating in mines. In mines below 1500 m, we encountered bats in approximately 25% of mines >3 m in length. Above 1500 m elevation, approximately 50% of mines > 3 m in length contained at least 1 bat. These estimates of mine use are based upon our general impressions only, because it was not possible (or deemed safe) to enter every mine, or to survey every part of the mines we did enter.

Species Accounts

Tadarida brasiliensis

T. brasiliensis was found at the lower elevations of the Inyo Mountains and southernmost portion of the White Mountains (lower Cottonwood Creek, above Oasis Ranch, Mono Co., California; T5S R37E, Sec 33; 1600 m). We observed a dispersed colony of 1028 at the base of McElvoy Canyon on the east side of the Inyo Mountains, Inyo Co., California (640 m). We describe this colony as "dispersed" because they roost in a series of overhanging ledges along the narrow canyon wall, rather than a single site. A perennial stream flows through the canyon below the roosts. We counted these bats on 26 July 1992 as they flew overhead after emerging, heading in the direction of Saline Valley. This site appears vacant during winter. A crevice in a large boulder above the Deep Springs dairy (Inyo Co., California; T7S R36E, Sec 1; 1590 m) hosts more than 100 *T. brasiliensis* for several weeks during the spring, perhaps a stopover during migration. On 19 August 1996 we found a small colony at the entrance of a dolomite mine at the western base of the Inyo Mountains near the "shoreline" of Owens Dry Lake, Inyo Co., California. We could not determine the number of bats in this colony, but from the limited guano deposit and apparent configuration of the crevice, perhaps no more than several dozen were present.

Euderma maculatum

Three *E. maculatum* were captured along lower Cottonwood Creek on the east side of the White Mountains (Mono Co., California; T5S R37E, Sec 33; 1600 m), 2 males on 17 August 1993 and 1 female on 14 August 1995. Based upon audible calls of this species, we found it to be a common forager among mid-elevation riparian corridors of the range down to the Owens Dry Lake bed (Inyo Co., California; west side of Inyo Mountains, 1080 m). We would typically hear *E. maculatum* from shortly after twilight until the early morning hours. From April through October we routinely heard *E. maculatum* foraging over the fields and buildings of Deep Springs College (Inyo Co., California; T7S R36E, Sec 1; 1600 m). The latest in the year this bat was heard at Deep Springs College was 9 November 1996.

Corynorhinus townsendii

Three foraging *C. townsendii* were captured during this survey, 1 male in Queen Canyon at the northern end of the White Mountains on 9 July 1992 (Esmeralda Co., Nevada; T1N R33E, Sec 32; 2410 m), 1 male at Lower Cottonwood Creek on the east side of the White Mountains on 27 August 1992 (Mono Co., California; T6S R37E, Sec 5; 1600 m), and 1 female on 25 July 1992 at a concrete water trough at the northwest end of Saline Valley Lake at 305 m (Inyo Co., California; T14S R38E, Sec 27). We observed 36 individuals exiting a maternity roost at the base of the White Mountains in Deep Springs Valley (Inyo Co., California; 1705 m), and a single male carcass was found in a building at Oasis Ranch in Fish Lake Valley on the east side of the White Mountains (Mono Co., California; T5S R37E, Sec 28; 1530 m). A maternity colony of several hundred is known on the west side of the White Mountains, Inyo Co., California (1710 m; Patricia Brown-Berry, personal communication). This bat is also known to roost in lava tube caves on the western slope of the Inyo Mountains at approximately 1380 m (Denyse Racine, California Department of Fish and Game, personal communication). The remaining *C. townsendii* observations were of hibernating individuals. Six bats were observed hibernating in a White Mountain mine at 3188 m on 28 November 1992, the highest observation of this survey. The majority of mines we entered during the winter months above 1500 m harbored at least 1 *C. townsendii*. This bat distributed itself well among the available hibernaculae, rather than concentrating within a few selected sites. The 7 largest concentrations observed (per mine) were 80, 51, 40, 25, 25, 20, and 19 bats. The group of 80 was found in the Inyo Mountains at 2140 m elevation with an air temperature near the bats of 5°C on 12 February 1995. The group of 51 was found in the White Mountains at 2400 m elevation and an air temperature near the bats of 4°C on 12 February 1994 (Inyo Co., California). Seven individuals were found in a mine complex on the west side of the White Mountains on 25 February 1993 (Mono Co., California). We observed these bats in a lower adit with an air temperature near them of –3°C.

Antrozous pallidus

We found *A. pallidus* at scattered locations throughout the Inyo Mountains below 1710 m and as low as 430 m at Saline Valley Hot Springs (Inyo Co., California; T13S R39E, Sec 18). Our only observations of this bat in the White Mountains occurred at lower Cottonwood Creek (Mono Co., California; T5S R37E, Sec 33; 1600 m). There is a maternity roost in a side entranceway of the Deep Springs College boardinghouse (Inyo Co., California; 1600 m) from which we counted 39 bats exiting on 5 August 1994. Bats, presumably from this colony, can often be seen night roosting at various sites around the college during the summer. This roost remains vacant during the winter. We captured 1 male and 1 female on 18 June 1996 and another female on 9 July 1996 on the eastern shore of Owens Dry Lake north of the town of Keeler (Inyo Co., California; T16S R38E, Sec 31; 1080 m).

Lasionycteris noctivagans

We captured a male *L. noctivagans* in the White Mountains at the lower Cottonwood Creek site (Mono Co., California; T5S R37E, Sec 33; 1600 m) on 11 June 1996. A female *L. noctivagans* was captured in a dormitory room at Deep Springs College (Inyo Co., California; T7S R36E, Sec 1; 1600 m) on 8 October 1991. On 5 December 1991 we observed an individual hibernating in a drill hole in a mine developed in dolomitic marble on the southern slope of the White Mountains (Inyo Co., California; 2050 m). Another individual was captured in the dormitory wing of Deep Springs College on 18 February 1995. From the condition of this bat and the time of year, it had probably aroused from hibernating on site.

Lasiurus cinereus

We captured 1 female and 3 males at 2090 m along Chiatovich Creek (Esmeralda Co., Nevada; T1S R34E, Sec 29) on 6 July 1992, and 17 females and 7 males at 1590 m along Cottonwood Creek (Mono Co., California; T5S R37E, Sec 33), both on the east side of the White Mountains. Another male was captured on 26 June 1992 along Wyman Creek at 1920 m on the southern reach of the White Mountains (Inyo Co., California; T6S R36E, Sec 22). These drainages all have stands of cottonwood (*Populus fremontii*), a large-leafed tree considered desirable to this tree-roosting species (Barbour and Davis 1969).

Pipistrellus hesperus

P. hesperus is the most common bat we captured in mist nets. Most captures occurred within the 1st hour after sunset. On 26 July 1992 we netted 51 females and 37 males at a pool in McElvoy Canyon on the east side of the Inyo Mountains in 1.5 h (Inyo Co., California; T14S R37E, Sec 1; 790 m). We often observed this species emerging well before dark. Our highest elevation capture was a male on 22 July 1992 at 2740 m in the Inyo Mountains at Mexican Spring (Inyo Co., California; T15S R38E, Sec 34). *P. hesperus* is known to be sporadically active throughout the winter (Barbour and Davis 1969), and we observed it in the late afternoon and early evening flying over and coming down to sip from the hot spring pools in Saline Valley, east of the Inyo Mountains, in February and March 1994 (Inyo Co., California; T13S R39E, Sec 18). Over the course of 7 nights between 6 April 1996 and 18 September 1996, we captured 30 *P. hesperus* over small ponds on the eastern shore of Owens Dry Lake near the town of Keeler (Inyo Co., California; T16S R38E, Sec 31; T17S R38E, Sec 5; T17S R38E, Sec 22; all at 1080 m). Our 4 hibernation observations of this bat occurred at the lowest mines we surveyed (1340–1400 m; Inyo Co., California). Air temperature near the bats in these mines was warmer (15°C) than temperatures we encountered at higher elevations, a situation not ideal for minimizing energy expenditure during torpor, but perhaps conducive to foraging during occasional winter mild spells (Barbour and Davis 1969, O'Farrell and Bradley 1970).

Eptesicus fuscus

We captured *E. fuscus* along the lower sections of perennial streamflows of the White Mountains. All drainages in which we captured this bat were upstream from ranches with established agricultural fields. Hock (1963) listed this bat as occurring up to 3090 m in the White Mountains. Unfortunately, we do not know whether this referred to a hibernating or foraging individual. On 26 June 1993 we found *E. fuscus* foraging along Lone Tree Creek on the west side of the White Mountains at 2070 m (Mono Co., California; T3S R33E, Sec 33). We found a single hibernating bat in a mine tunnel in the White Mountains on 12 February 1994 at 2500 m (Inyo Co., California). A storage shed at Deep Springs College (Inyo Co., California; T7S R36E, Sec 1; 1600 m) serves as a night roost for about 3 dozen of these bats; however, the day roost location for this group remains unknown. On 16 August 1996 we captured a post-lactating female over a small pond on the eastern shore of Owens Dry Lake (Inyo Co., California; T16S R38E, Sec 31; 1080 m).

Myotis evotis

We found *M. evotis* along the lower drainages of the White Mountains and up through the pinyon-juniper zone. Our highest capture for this species occurred on 8 July 1993 at 2470 m along Chiatovich Creek (Esmeralda Co., Nevada; T1S R33E, Sec 35), where we captured 1 male and 1 female; however, the MVZ lists a 1954 record from Cottonwood Creek (White Mountains, Mono Co., California) at 2895 m. A female *M. evotis* was captured beside a storage building at Deep Springs College (Inyo Co., California; T7S R36E, Sec 1; 1600 m) on 4 September 1992. All other captures were at water sites.

Myotis volans

M. volans was well distributed throughout the White–Inyo Range in the Great Basin scrub and pinyon-juniper zones. We observed a single hibernating *M. volans* during this survey in a mine at the north end of the White Mountains on 31 January 1993 (Esmeralda Co., Nevada; 2770 m). Our highest foraging observation of *M. volans* occurred at Mexican Spring toward the southern end of the Inyo Mountains at 2740 m (Inyo Co., California; T15S R38E, Sec 34); however, the MVZ also lists a 1954 record of "many" specimens of this bat from Cottonwood Creek (White Mountains, Mono Co., California) at 2895 m. Our lowest capture of this bat was a male netted on 25 August 1992 at a road stream crossing in Silver Canyon on the west side of the White Mountains at 1410 m (Inyo Co., California; T6S R34E, Sec 24). On 19 June 1996 we captured a nonreproductive female over a small pond on the eastern shore of Owens Dry Lake near the town of Keeler (Inyo Co., California; T17S R38E, Sec 5; 1080 m).

Myotis californicus

We captured *M. californicus* at 4 sites in the White Mountains along its lower slopes in the Great Basin scrub zone and up into the beginning of the pinyon-juniper zone. On 24 July 1995 and 3 August 1995, a female *M. californicus* was found roosting during the day in a classroom at Deep Springs College (Inyo Co., California; T7S R36E, Sec 1; 1600 m). On 25 August 1992 we captured a female at a road stream crossing in Silver Canyon on the west side of the White Mountains (Inyo Co., California; T6S R34E, Sec 24; 1410 m) and 2 males at the Lone Tree Creek headworks (Mono Co., California; T3S R33E, Sec 33; 2070 m), also on the west side of the White Mountains. Three other females were captured along the lower portion of Cottonwood Creek on separate occasions (Mono Co., California; T5S R37E, Sec 33; 1660 m).

Myotis ciliolabrum

Together with *C. townsendii*, *M. ciliolabrum* was the only other bat we commonly found hibernating in the White–Inyo Range. Our highest hibernating observation of *M. ciliolabrum* occurred on 12 February 1994 at 2500 m in the White Mountains (Inyo Co., California), and our lowest was on 23 December 1990 at 1710 m in a small mine on the northwest slope of Deep Springs Valley (Inyo Co., California). We usually found this bat well up into a crevice and hibernating alone, even among a group of tunnels. However, we found 10 distributed through a mine in Marble Canyon on the east side of the Inyo Mountains (Inyo Co., California; 2260 m). We found *M. ciliolabrum* foraging throughout the Great Basin scrub and pinyon-juniper zone of the range. Our highest foraging observation for this species was a male captured at Mexican Spring toward the southern end of the Inyo Mountains on 22 July 1992 at 2740 m (Inyo Co., California; T15S R38E, Sec 34); the lowest was a pregnant female we captured over the runoff of a spring on the eastern shore of Owens Dry Lake (T17S R38E, Sec 9; 1080 m) on 30 May 1996.

Myotis lucifugus

We did not encounter *M. lucifugus* during our survey, but the LACM lists a specimen of *M. lucifugus* from lower Wyman Canyon in the southern White Mountains from May 1972 (Inyo Co., California; T6S R36E, Sec 23; 1740 m). However, we believe a discrepancy exists regarding the *Myotis* species in the Owens Dry Lake area. Our comments in this regard are in the Discussion below.

Myotis yumanensis

We captured 24 specimens of this bat along the eastern shore of Owens Dry Lake on the southern end of the Inyo Mountains. The most prolific activity occurred over a small pond several km north of the town of Keeler (Inyo Co., California; T16S R38E, Sec 31; 1080 m). There we captured 8 lactating females and 1 volant juvenile male on 9 July 1996. At another small pond closer to Keeler, we captured 1 lactating and 1 pregnant female on 19 June 1996 (Inyo Co., California; T17S R38E, Sec 5; 1080 m). These records indicate the presence of a maternity roost in the Keeler vicinity. On 24 August 1995 we netted a female at the Sulfate Well on Owens Dry Lake (Inyo Co., California; T17S R38E, Sec 18) and a male and a female on 14 September 1995 near the eastern Owens Lake margin (Inyo Co., California; T16S R37E, Sec 26). We also observed these bats flying to foraging sites on the lake bed at dusk, presumably heading out from roost sites east of the lake, at the base of the Inyo Mountains.

DISCUSSION

Of the 13 bat species we encountered in this survey, none specialized in any of the 5 vegetation zones of the White–Inyo Range. All species overlapped with at least 1 other zone, although for *L. noctivagans*, *L. cinereus*, and *M. californicus* the overlap from the Great Basin desert scrub into the pinyon-juniper zone was limited. *E. maculatum*, *C. townsendii*, *P. hesperus*, *E. fuscus*, and *M. volans* were all found foraging over 3 zones. Including the hibernating observations, *C. townsendii* extended its range through all zones in which we observed bats. We observed only *E. fuscus* and *M. volans* foraging in the higher bristlecone–limber pine zone, compared with 9 foraging species in the pinyon-juniper zone. In contrast, Morrison et al. (1993) observed 61 bird species in the bristlecone–limber pine zone, 3 more than in the pinyon-juniper zone. The reduced bat foraging activity in the bristlecone–limber pine zone may result from the diurnal vs. nocturnal habits of birds vs. bats and these bats' exclusive insect diet. The higher elevation of the bristlecone–limber pine zone elicits colder nocturnal temperatures, causing impoverished nocturnal insect activity (Wellington 1945). Graham (1983) found a similar decrease in bat species moving up an elevational gradient in the Peruvian Andes.

C. townsendii foraged in 3 different vegetation communities (Fig. 1). This bat is a known lepidopteran specialist (Barbour and Davis 1969, Clark et al. 1993). While some lepidopteran species may be found throughout these vegetation communities, the overall species composition among these communities most likely differs. Successfully utilizing such different environments as Mojave mixed desert scrub and pinyon-juniper forest suggests an ability to exploit a variety of foraging strategies and prey selection. Such adaptability may seem surprising in view of evidence that this species remains threatened over much of its original range (former C2 species and California species of special concern). However, this result is consistent with other studies indicating that roost disturbance may be a more decisive factor in this bat's decline than habitat disturbance (Pierson and Rainey 1994). The remoteness and low human population density of the White–Inyo Range reduce human disturbance as a factor. However, the remoteness of this range also provides relatively undisturbed foraging habitat; thus, the relative effect of roost vs. habitat disturbance cannot be separated. In fact, the situation in the White–Inyo Range could also be interpreted to suggest that *C. townsendii* requires undisturbed roosts *and* foraging habitat to thrive. Interestingly, the modern White–Inyo population of *C. townsendii* may exceed prehistoric numbers. Humphrey and Kunz (1976) concluded that this bat is a capable colonizer. It naturally roosts in caverns, which rarely occur in this range. Because of this, *C. townsendii* has only recently begun roosting in the area, basically within the many mines created in the last century.

We should note that our survey shows a bias toward activity in riparian corridors and other areas with water, as those were the only places in which we could effectively capture foraging bats. With this bias, the comparative richness we measured in the Great Basin desert scrub zone may instead depict the richness of a wetland environment in the milder climate of this lower elevation zone compared with the others. Thus, it may not accurately reflect general comparative trends in species richness in these zones. Bats typically sip water by skimming over it (Kunz 1982) and thus require water sources with an open surface. We visited point water sources in the Inyo Mountains with such constant bat activity that we did not risk setting mist nets too near them. Because such water sources are the only ones available for many kilometers in any direction, it seems clear that entire populations depend upon these isolated sources. We recommend that wildlife management planners consider the impacts of such water sources upon bats, in addition to other wildlife. For example, the seemingly harmless cessation of water flow to an old trough may profoundly affect bat populations in a large surrounding area. Evaluation of existing and planned water sources with consideration of bat needs could do much to enhance bat populations in arid regions.

Overall, *C. townsendii* and *M. ciliolabrum* accounted for nearly 99% of all bats found in mines, with *C. townsendii* comprising about 89%. Because both *E. fuscus* and *M. volans* are regarded as regular mine users (Tuttle and Taylor 1994), the single hibernation sightings for these bats contrasted with our foraging observations of these species. This indicated that either their White–Inyo hibernaculae remain undiscovered or they typically leave the area to hibernate. Our observation of *L. noctivagans* hibernating in a mine is of note because this species has rarely been found to use mines as hibernaculae (Barbour and Davis 1969, Altenbach and Pierson 1994).

Noticeably absent from this survey was *M. lucifugus*, whose range is described as encompassing the White–Inyo Range (Hall 1981). Perhaps the sparse timber of the range does not meet the requirements of *M. lucifugus*, which is described as preferring timbered areas (Hall and Kelson 1959). The LACM record from lower Wyman Canyon may be representative of occasional forays this species may make into the White–Inyo Range from the Sierra Nevada to the west. The thoroughness of the present survey would have likely encountered this species if it routinely inhabited the White–Inyo Range.

The Owens Lake myotid that we recorded as *M. yumanensis* is described by Harris (1974) as the subspecies *M. lucifugus relictus*, with Keeler as the type location. However, consistent with earlier descriptions but contrary to Harris, we prefer to maintain its designation as *M. yumanensis* based upon the dull and pale pelage and light-colored ears characteristic of *M. yumanensis*, and our field observations in which its habitat and foraging behavior are more consistent with *M. yumanensis* than with *M. lucifugus*. The Keeler/Owens Dry Lake locale is unforested, an uncharacteristic habitat for *M. lucifugus*. From our observations these bats foraged almost exclusively over the scattered open water along the margin of Owens Dry Lake, flying just over it, a strategy typical of *M. yumanensis* (Barbour and Davis 1969, Herd and Fenton 1983). Harris's conclusion was based solely upon 10 museum specimens, a "few" study skins, and specimens in alcohol. "Few specimens of *M. l. relictus* are undamaged, resulting in a less than ideal sample size for statistical analysis." Harris, noting the pale coloration of the Keeler specimens, accounted for it by stating that "selection at the lower elevations could easily have produced the level of paleness seen at Keeler." Lending further confusion, Harris identified 3 of the 10 Owens Lake museum specimens as *M. yumanensis*. Whatever the taxonomic resolution of this debate, all bats we recorded as *M. yumanensis* are a morphologically similar population. A definitive resolution of the species designation for this population may await DNA analysis.

M. thysanodes (fringed myotis) was also absent from this survey but has a range described to include the White–Inyo Range (Hall 1981). Barbour and Davis (1969) described *M. thysanodes* as preferring pinyon-juniper forests, making their absence from the White–Inyo Range more conspicuous. However, Hall and Kelson (1959) mentioned that it does not seem to be common anywhere in its range and that it seems to prefer caves, which seldom occur in the range. Thus, in contrast to *C. townsendii*, which has apparently moved into the range by exploiting many available mines in place of natural caves, *M. thysanodes* may not be as adaptable to mines or may move more slowly into previously unused areas.

More than a dozen bat species inhabit the White–Inyo Mountain Range, attracted by a variety of natural and artificial conditions. Our data indicate influences in species distribution from vegetation zones, availability of water, and mines. Further work using noncontact census methods will be required to assess the impact of vegetation zones away from water. Today the White–Inyo Range serves as a refuge for bats, and careful management of water, mines, and other resources may continue this role indefinitely.

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HABITAT USE BY SMALL MAMMALS IN SOUTHEASTERN UTAH, WITH REFERENCE TO MEXICAN SPOTTED OWL MANAGEMENT

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ABSTRACT.—We determined temporal and spatial differences in abundance and habitat use by small mammals in southeastern Utah as part of an effort to enhance management of the Mexican Spotted Owl (*Strix occidentalis lucida*), listed by the federal government as threatened. Woodrats (*Neotoma* spp.) were captured only in canyons and most frequently in the pinyon-juniper (*Pinus edulis–Juniperus osteosperma*) vegetation type. White-footed mice (*Peromyscus* spp.) were found in a variety of vegetation types in both canyons and mesas. The deer mouse (*P. maniculatus*) was generally the most frequently captured species among vegetation types. We found seasonal and yearly differences in relative abundance of each small mammal species. Our data suggest that the pinyon-juniper vegetation type within canyons is an important component of Mexican Spotted Owl habitat.

Key words: small mammals, habitat use, Utah, rodents, Mexican Spotted Owl.

Since its federal listing as a threatened species in April 1993, several authors have reported on habitat requirements of the Mexican Spotted Owl (Ganey 1994, Zwank et al. 1994, Ward and Block 1995). It has been suggested that Mexican Spotted Owls select habitats based partially on the availability of prey (Ward and Block 1995). Confirming this theory is vital for the owl's recovery; however, we know of no published studies examining the distribution and abundance of predominant prey species within the range of the Mexican Spotted Owl in Utah. In southeastern Utah these owls occur >75% of the time within canyons and <25% of the time on mesa tops (Willey 1992); they forage primarily in the pinyon-juniper (*Pinus edulis–Juniperus osteosperma*) vegetation type within canyons (Willey 1992, unpublished data).

Our objective was to determine spatial and temporal differences in abundance and habitat relationships of small mammals in canyons and on mesas of the Manti-LaSal National Forest in southeastern Utah. These data can then be used to aid in managing and recovering the Mexican Spotted Owl in Utah.

STUDY AREA

We conducted our study on the Monticello Ranger District of the Manti-LaSal National Forest, San Juan County, Utah. The area, considered part of the Canyonlands Section of the Colorado Plateau geographic province (Thornbury 1965:417, 426), ranges from elevations of approximately 1830 to 2680 m. Elk Ridge, the dominant topographic feature of the study area, is flanked to the west and east by steep-walled canyons, 3 of which (Texas, Hammond, and Dark canyons) contain Mexican Spotted Owls (Willey 1992) and are the focus of our study. The study area comprises extensive sandstone canyonlands, stair-step benchlands, alluvial valleys, high plateaus, and laccolithic mountains (Barnes 1978).

Vegetation types sampled in our study area were selected based on their predominance within canyons and on mesas. Within canyons the following vegetation types were sampled: (1) pinyon-juniper woodlands, (2) mixed-mountain brush (Gambel oak [*Quercus gambelii*], alderleaf mountain-mahogany [*Cercocarpus montanus*], and Utah serviceberry [*Amelanchier utahensis*]), (3) riparian (willow [*Salix*] spp., grasses, and forbs), and (4) mixed-conifer (ponderosa pine [*Pinus ponderosa*], white fir [*Abies concolor*], and Douglas-fir [*Pseudotsuga menziesii*]). We sampled 3 vegetation types on mesas: mature ponderosa pine, aspen- (quaking aspen [*Populus tremloides*]) ponderosa pine, and grass/forb-shrub.

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METHODS

Small-mammal trapping grids were located randomly within activity areas of 3 owl home ranges in Texas, Hammond, and Dark canyons; activity areas were delineated following Willey (unpublished data). Trapping grids were set within each of the predominant vegetation types in canyons and on mesas surrounding each canyon. Because canyon width varied from approximately 100 to 300 m, to fit a grid completely within some of the designated canyon vegetation types, we used grids of various lengths and widths. However, we arranged them to approximate as nearly as possible a 5 × 5 trapping pattern; all mesa grids were 5 × 5. We separated all trapping stations by 15 m.

We trapped during 2 seasons for 2 yr, summer and fall 1994 and 1995. Summer trapping was done from May through early August, fall trapping from late August through October. In 1994 we trapped 35 grids in each season (5 grids/vegetation type; 20 grids in canyons [Hammond and Texas canyons], 15 grids on mesa tops). In 1995, 28 grids were trapped in each season (3–5 grids/canyon vegetation types, 4 grids/mesa vegetation types; 16 grids in canyons [Hammond, Texas, and Dark canyons], 12 on mesas). A grid from each vegetation type was trapped synchronously during a sampling session to lessen temporal biases in results. Each trapping period ran for 4 nights. O'Farrell (1974) found that the moon had a negative effect on nocturnal rodent activity; therefore, we trapped only on nights around a new moon (10 nights before, 10 nights after).

We placed 2 Sherman live-traps at each trapping station, alternating placement of extra-large (10 × 12 × 37-cm) traps at each trapping station within each grid, so that 13 trapping stations consisted of 1 extra-large trap and 1 large (7.6 × 8.2 × 22.9-cm) trap and 12 trapping stations consisted of 2 large traps. All traps contained polyester batting and were baited with rolled oats and peanut butter (Davis 1982). Extra-large traps increased the probability of capturing woodrats.

We set traps before sunset and checked them at sunrise. Upon capture, all mammals were identified to species, aged, sexed, weighed, and individually identified by toe-clipping. We differentiated between juveniles and adults by pelage coloration, and we recorded reproductive condition as nonreproductive, abdominal testes, or nipples.

We estimated relative abundance of predominant prey species as catch-per-unit effort, defined as the number of captures per 100 trap-nights. Trap-nights were defined as the number of traps per night multiplied by the number of nights in the field minus sprung-but-empty traps (Mills et al. 1991).

We made the following comparisons of relative abundance of each species: (1) separately for canyons and mesas between years, between seasons between years, and between seasons within years; (2) for canyons versus mesas within years and for each season within each year; and (3) between vegetation types separately for canyons and mesas for each season within each year. These analyses provide information on temporal and spatial differences in species abundance and habitat use. We used a Mann-Whitney test (Zar 1984:138–146) for comparisons of relative abundance of predominant prey species between 2 groups. For comparisons between more than 2 groups, such as between vegetation types, the Kruskal-Wallis test (Zar 1984:201–202) was used. If a significant difference was found between vegetation types, we used Dunn's test (Zar 1984:200) to determine where the difference occurred. Because of violations of assumptions, we did not conduct parametric analyses, and we avoided multivariate analyses because of low sample sizes for some comparisons (exploratory multivariate analyses indicated no substantial differences in interpretations with analyses presented herein). $P < 0.01$ was used for significance because of repeated 2-way comparisons; results at $0.01 < P < 0.05$ were discussed as tendencies toward significance (exact *P*s are provided to aid in interpretation of results).

RESULTS

Species Composition

During 25,148 trap-nights we captured a total of 2906 new animals. White-footed mice (*Peromyscus* spp.) were the most frequently captured species group (81.2% of all captures), of which 75.0% were deer mice (*P. maniculatus*), 11.7% canyon mice (*P. crinitus*), 10.0% brush mice (*P. boylii*), and 3.3% pinyon mice (*P. truei*). Woodrats (*Neotoma* spp.) were captured only in canyons and represented 1.9% of all captures, of which 80.4% were Mexican (*N. mexicanus*), 14.3% white-throated (*N. albigula*), and 5.4% bushy-tailed (*N. cinerea*) woodrats. The montane vole (*Microtus montanus*), least chipmunk (*Tamias minimus*), Colorado chipmunk (*T. quadrivittatus*), rock squirrel (*Spermophilus variegatus*), silky pocket mouse (*Perognathus flavus*), western harvest mouse (*Reithrodontomys megalotis*), ord kangaroo rat (*Dipodomys ordii*), and a shrew species (*Sorex* spp.) represented 16.9% of all captures.

Seasonal and Yearly Variation

Relative abundance (see Table 1) of deer mice on mesas was significantly greater in fall 1995 than fall 1994 ($P = 0.01$, Mann-Whitney [M-W]) and in fall 1995 than summer 1995 ($P < 0.0001$, M-W). Relative abundance of deer mice in canyons tended to be greater in summer 1994 than summer 1995 ($P = 0.04$, M-W). Relative abundance of canyon mice in canyons was significantly greater in 1994 than 1995 ($P < 0.0001$, M-W) and in fall 1994 than fall 1995 ($P = 0.0001$, M-W), and tended to be greater in summer 1995 than summer 1994 ($P = 0.0250$, M-W). Relative abundance of brush mice in canyons was significantly greater in 1995 than 1994 ($P < 0.0001$, M-W), in summer 1995 than summer 1994 ($P < 0.0001$, M-W), and in fall 1994 than summer 1994 ($P = 0.0001$, M-W). In canyons relative abundance of Mexican woodrats tended to be greater in summer 1995 than summer 1994 ($P = 0.04$, M-W) and was significantly greater in fall 1994 than fall 1995 ($P = 0.005$, M-W) and in fall 1994 than summer 1994 ($P = 0.0013$, M-W).

Canyons Versus Mesas

The deer mouse was significantly more abundant on mesas during 1995 ($P = 0.0001$, M-W; Table 1). The canyon mouse and pinyon mouse were significantly more abundant in canyons during 1994 ($P < 0.0000$, $P = 0.007$, respectively, M-W; Table 1), whereas the brush mouse was significantly more abundant in canyons the next year ($P < 0.0000$, M-W; Table 1).

The deer mouse had a significantly higher relative abundance on mesas during summer and fall 1995 ($P = 0.0168$, $P < 0.0001$, respectively, M-W; Table 1). The canyon mouse had a significantly higher relative abundance in canyons during summer 1994 ($P = 0.0007$, M-W; Table 1). The canyon mouse was captured only in canyons in fall 1994 and summer 1995, and only on mesas in fall 1995 (Table 1). The brush mouse had a significantly higher relative abundance in canyons during fall 1994 ($P = 0.0007$, M-W) and during summer and fall 1995 ($P = 0.0010$, $P = 0.0021$, respectively, M-W; Table 1). The Mexican woodrat was captured only in canyons (Table 1).

Mesa Vegetation Types

We observed a tendency for differences in relative abundance of deer mice within mesa vegetation types during summer and fall 1994 ($P = 0.017$, $P = 0.031$, respectively, Kruskal-Wallis [K-W]; Table 2) and fall 1995 ($P = 0.05$, K-W; Table 2). Due to large variances in abundance numbers, we could not determine where the differences occurred in statistical analyses of multiple comparisons. Upon visual examination of mean indices, we determined the grass/forb-shrub vegetation type had a higher relative abundance of deer mice than the aspen or ponderosa pine vegetation types. Canyon mice, brush mice, and pinyon mice were captured very infrequently on mesas, and we captured no Mexican woodrats on mesas.

Canyon Vegetation Types

We observed a tendency for differences in relative abundance of brush mice between canyon vegetation types in fall 1994 ($P = 0.021$, K-W; Table 2). Visual examination indicates that the pinyon pine and mixed-mountain brush vegetation types had a higher relative abundance of brush mice than did the other vegetation types. We observed significant differences in relative abundance of pinyon mice in fall 1994 ($P = 0.005$, K-W) and summer 1995 ($P = 0.01$, K-W). Statistical analyses of multiple comparisons could not determine where the difference occurred due to large variances in abundance numbers. Visual examination of mean indices shows that the pinyon-juniper vegetation type had the highest relative abundance of pinyon mice in both seasons (Table 2). We observed no other significant differences in relative abundance of other species within canyon vegetation types. Mexican woodrats were captured 48.9% of the time in pinyon-juniper within canyons, whereas 24.4% were captured in mixed-mountain brush, 22.2% in the riparian type, and 8.9% in mixed-conifer.

TABLE 1. Small mammal relative abundance (no. animals per 100 trap-nights) estimates in canyons and mesas of the Manti-LaSal National Forest, Utah, during summer and fall 1994 and 1995.

	1994						1995					
	Summer		Fall		Overall		Summer		Fall		Overall	
Species	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
Deer mouse												
Mesas	8.7	5.18	6.1	6.62	7.4	5.99	7.9	4.43	13.0	6.40	10.1	5.81
Canyons	5.7	2.41	7.1	6.07	6.4	4.62	4.0	2.67	5.0	3.04	4.6	2.82
Canyon mouse												
Mesas	<0.1	0.13	0.0		0.0	0.09	0.0		<0.1	0.17	0.0	0.11
Canyons	2.2	2.41	3.7	4.12	3.0	3.42	1.2	2.19	0.0		0.7	1.69
Brush mouse												
Mesas	0.1	0.18	<0.1	0.13	0.1	0.15	0.5	1.62	0.3	0.56	0.4	1.25
Canyons	0.1	0.37	1.4	1.46	0.4	0.82	3.4	2.51	2.6	2.08	2.7	1.42
Pinyon mouse												
Mesas	0.1	0.18	0.0		0.0	0.13	0.2	0.44	0.1	0.22	0.1	0.36
Canyons	0.4	1.07	0.3	0.49	0.4	0.82	0.4	0.91	1.0	1.83	0.7	1.42
Mexican woodrat												
Mesas	0.0		0.0		0.0		0.0		0.0		0.0	
Canyons	0.2	0.59	0.7	0.75	0.4	0.72	0.3	0.38	0.3	0.32	0.2	0.32
Other species												
Mesas	1.8	2.50	1.5	1.91	2.3	1.68	2.8	1.95	3.7	3.26	4.5	2.49
Canyons	0.6	0.83	0.6	0.91	0.6	0.86	1.3	1.48	2.1	1.76	1.8	1.65

DISCUSSION

The deer mouse was generally the most frequently captured species in all vegetation types surveyed, which is consistent with its general habitat associations (Burt and Grossenheider 1976, Hoffmeister 1986, Fitzgerald et al. 1994). Fitzgerald et al. (1994) noted that where habitat-specific *Peromyscus* spp. occur, deer mice will be locally scarce or absent. This was not the case in our study, where in most vegetation types deer mice were consistently more abundant than any other *Peromyscus* spp. However, Armstrong (1979) noted that it is not uncommon for *Peromyscus* species to co-occur in areas of heterogeneous vegetation, as are found within canyons in our study area. For example, the mixed-conifer vegetation type within canyons may have scattered pinyon pines or patches of Gambel oak within them. Thus, the general heterogeneous distribution of vegetation types in our study area may explain why deer mice were consistently abundant in all vegetation types.

The canyon mouse was captured in all canyon vegetation types in each season of each year except in fall 1995, when they were not captured in any vegetation type. The canyon mouse is generally associated with rocky, slickrock, and cliff habitats (Hoffmeister 1986, Johnson and Armstrong 1987, Fitzgerald et al. 1994). Thus, the widespread presence of rocky substrates within most vegetation types may explain the presence of this species in all vegetation types. Johnson and Armstrong (1987) noted that vegetation in an area may have little or no effect on local distribution of this species, but that the species is associated with the area's rocky substrate rather than with the plant association.

The brush mouse was most frequently captured in the pinyon-juniper vegetation type in canyons, which is consistent with previous descriptions of the species' habitat (Wilson 1968, Hoffmeister 1986, Fitzgerald et al. 1994). It was also abundant in the riparian vegetation type where streambeds consist of heavy brush and rocks. The pinyon mouse was most frequently captured in pinyon-juniper, once again consistent with previous descriptions of the species' habitat throughout its range (Wilson 1968, Burt and Grossenheider 1976, Armstrong 1979, Hoffmeister 1986, Fitzgerald et al. 1994).

We captured the Mexican woodrat in the pinyon-juniper vegetation type in all seasons sampled. In 3 of the 4 seasons sampled, it was captured in mixed-mountain brush and riparian vegetation, and in 2 of the 4 seasons in mixed-conifer. Our results are consistent with literature on Mexican woodrat habitat: it is

TABLE 2. Relative abundance (no. animals per 100 trap-nights) estimates of small mammals within mesa and canyon vegetation types of the Manti-LaSal National Forest, Utah, during summer and fall 1994 and 1995.

	1994				1995			
	Summer		Fall		Summer		Fall	
Species	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
MESAS								
Deer mouse								
Aspen	6.3	4.33	2.7	2.81	6.5	3.47	10.6	1.42
Ponderosa pine	6.1	3.11	2.5	2.49	5.9	4.52	9.3	1.66
Grass/forb-shrub	13.7	4.30	13.0	7.06	11.3	4.10	19.0	8.68
CANYONS								
Deer mouse								
Mixed-conifer	4.8	2.38	7.7	3.56	3.2	2.08	4.9	3.44
Pinyon-juniper	5.5	1.53	1.5	1.41	3.6	2.69	5.5	3.59
Mixed-mountain brush	6.2	3.20	9.7	7.73	5.5	3.56	6.8	3.16
Riparian	6.1	2.81	9.6	6.69	4.4	3.51	3.9	1.32
Canyon mouse								
Mixed-conifer	1.8	2.49	1.6	2.22	1.1	2.55	0.0	
Pinyon-juniper	3.1	3.00	6.3	5.76	0.6	0.97	0.0	
Mixed-mountain brush	2.5	2.89	4.2	4.16	1.7	2.94	0.0	
Riparian	1.5	1.46	2.9	3.24	1.9	3.23	0.0	
Brush mouse								
Mixed-conifer	0.0		0.6	0.82	2.0	1.71	1.0	0.71
Pinyon-juniper	0.3	0.72	2.2	1.83	4.0	3.61	3.0	2.60
Mixed-mountain brush	0.1	0.22	2.3	1.40	1.8	2.36	2.4	1.62
Riparian	0.0		0.4	0.65	4.0	0.62	3.4	0.67
Pinyon mouse								
Mixed-conifer	0.1	0.22	0.0		0.0		0.0	
Pinyon-juniper	1.3	1.94	0.9	0.43	1.2	1.35	3.0	2.41
Mixed-mountain brush	0.1	0.22	0.1	0.22	0.0		0.0	
Riparian	0.2	0.45	0.2	0.45	0.0		0.0	
Mexican woodrat								
Mixed-conifer	0.0		0.2	0.27	0.2	0.27	0.0	
Pinyon-juniper	0.5	1.12	1.3	0.98	0.3	0.49	0.3	0.50
Mixed-mountain brush	0.2	0.45	0.4	0.42	0.5	0.50	0.0	
Riparian	0.0		0.8	0.80	0.2	0.29	0.2	0.29

characteristically found on rocky slopes, cliffs, and rock outcrops (Burt and Grossenheider 1976) and is associated with pinyon-juniper woodlands (Armstrong 1979, Cornely and Baker 1986, Fitzgerald et al. 1994).

We found that canyon and brush mice were captured primarily within canyons, and the Mexican woodrat was captured only within canyons. As mentioned above, Mexican Spotted Owls studied in this area were located primarily (>75%) within canyons. Willey (unpublished data) found that owls within the canyons sampled were foraging primarily in pinyon-juniper. This corresponds with woodrat distribution and abundance in our study.

Our results should be useful in the development of management plans for the Mexican Spotted Owl. *Peromyscus* spp., the predominant prey species of the Mexican Spotted Owl (Ward and Block 1995), were captured in a variety of vegetation types within canyons, and woodrats were captured only in canyons. Thus, maintaining a mixture of vegetation types may provide a buffer against the effects of small mammal cycles in any particular vegetation type (Ward and Block 1995). Small mammal populations are known to fluctuate with seed and/or cone-crop production (McKeever 1961, Buchanan et al. 1990). If a small mammal species is not an extreme habitat specialist (as the owl's predominant prey species are not), owls may temporarily be able to move into food-abundant areas and maintain viable populations. Our results also suggest that the pinyon-juniper vegetation type is an important component of the Mexican Spotted Owl's home range during summer and fall based on owl foraging behavior studies and owl diet (Willey

1992, unpublished data) and the distribution and abundance of key species. Future research should address the correlation between owl survival and reproductive success and the amount of pinyon-juniper vegetation type within the home range of individual owl pairs.

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LATE PLEISTOCENE MICROTINE RODENTS FROM SNAKE CREEK BURIAL CAVE, WHITE PINE COUNTY, NEVADA

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ABSTRACT.—A total of 395 microtine rodent specimens recovered from Snake Creek Burial Cave (SCBC) are referred to *Microtus* sp. and *Lemmiscus curtatus*. Radiocarbon and Uranium series dates indicate an age for these fossils of between 9460 ± 160 yr. B.P. and 15,1000 ± 700 yr. B.P. The sample of lower first molars of *Lemmiscus* includes 4-, 5-, and 6-closed triangle morphotypes. Earlier reports of the 4-closed triangle morphotype are from Irvingtonian deposits in Colorado, Nevada, and New Mexico and from early Rancholabrean deposits in Washington. The morphotype is not known in living populations of *Lemmiscus*. SCBC specimens constitute the youngest record of the 4-closed triangle morphotype and are the only specimens reported from the late Rancholabrean. The time of disappearance of *Lemmiscus* with this molar morphology is unknown, but populations with this morphotype possibly became extinct at or near the end of the Pleistocene.

Key words: Lemmiscus, Microtus, *Pleistocene, extinction.*

Terrestrial vertebrate faunas of the Rancholabrean mammal age (late Pleistocene) from the central Great Basin have, for the most part, been discovered via exploration and excavation of cave deposits (Grayson 1993). Many of these localities are from relatively high elevations; fewer low-elevation sites have been discovered and consequently less is known of the Rancholabrean faunal history at lower elevations. Excavations in Snake Creek Burial Cave (SCBC), a natural trap cave from the southern Snake Range in White Pine County, Nevada, resulted in the recovery of an extensive vertebrate fauna consisting of over 30,000 skeletal elements (Mead and Mead 1989). The cave is formed in a small Devonian limestone ridge (separated from the mountains by a broad alluvial fan) at 1731 m elevation and is one of the few lowland sites in the Great Basin that has produced a late Pleistocene fauna.

Preliminary sampling in 1984 from the profile of a trench excavated by cavers produced a small vertebrate assemblage indicative of late Pleistocene age (Mead and Mead 1989). More extensive excavations were undertaken in 1987 when 4 contiguous 1 × 1-m test pits were excavated using arbitrary 10-cm stratigraphic levels to a depth of approximately 1 m below the present surface (2 m below an established datum point in the cave). Fossils recovered from the upper 25 cm (Unit I) are secondarily deposited as a result of digging activities by cavers. A bat guano layer (Unit II = level 3) marks the beginning of undisturbed deposits in the sequence. The highly fossiliferous Unit III (encompassing levels 4–10) produced the majority of vertebrates and is the presumed source of materials recovered from Unit I backdirt. The top of Unit III is radiocarbon dated at 9460 ± 160 yr. B.P. (radiocarbon years before 1950; dated material was bat guano), and a Uranium series date on an *Equus* (horse) phalanx from near the bottom of the excavation gave an age of 15,100 ± 700 yr. B.P. (Mead and Mead 1989).

Preliminary discussion of the fauna and more extensive treatments of reptilian and numerous mammalian mustelid carnivore remains were published previously (Mead and Mead 1985, Mead et al. 1989, Mead and Mead 1989). Many additional components of the small mammal fauna are under study now, and our purpose here is to document microtine rodents from the site.

A total of 395 specimens are referred to the 2 microtine rodent genera *Microtus* (voles) and *Lemmiscus* (sagebrush voles), both of which have rootless molars with a relatively complex

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occlusal surface. The lower 1st molar (M/1), lower 3rd molar (M/3), upper 3rd molar (M3/), and edentulous dentaries of these genera are usually readily identifiable and constitute the basis for this report.

DESCRIPTIVE ACCOUNTS

All specimens are curated into the collections of the Laboratory of Quaternary Paleontology, Quaternary Studies Program, Northern Arizona University (NAUQSP). Elements listed below are followed by the specimen number (or range of numbers). Dental terminology follows Repenning (1992).

Microtus sp. Schrank, 1798

MATERIAL.—Left dentary with M/1 and M/3: 7680; left dentary with I, M/1–2: 7702; right dentary with I, M/1–2: 7691; right dentary with I, M/2–3: 7890; isolated M/1: 7681–7690, 7692–7701, 7703–7733, 7872, 7874, 7876; isolated M/3: 7877–7889, 7891–7894, 7933–7936, 7938–7939; isolated M3/: 7837–7846, 7873, 7937; left edentulous dentary: 8045–8074; right edentulous dentary: 8019–8044.

DIAGNOSIS.—Primary wings on the lower 1st molar of *Microtus* species (in the restricted sense of Repenning 1987, 1992) are well developed and form triangles 4 and 5; secondary wings are usually present. In some extinct early North American representatives of this genus (placed in the species *M. paroperarius*) and the extant *M. oeconomus*, the lingual primary wing (triangle 5) of the lower 1st molar is generally open and broadly confluent with the anterior cap on which only a single secondary wing may be developed (Hibbard 1944, Youngman 1975, Hall 1981). In most other North American species, the lingual primary wing is closed, and development of secondary wings and morphology of the anterior cap are highly variable. For this reason specific identification of isolated teeth of *Microtus* species is problematic (Zakrzewski 1985). Multivariate statistical methods were shown to be useful in discriminating isolated molars of several species from the southwestern United States (Smartt 1977), but no comprehensive study of this kind that includes all North American species has yet been published. In the absence of such a study, reliable identification of many *Microtus* species remains impossible. Most of the lower 1st molars from SCBC have 5 closed triangles (Fig. 1A), but 4 individuals have a closed labial secondary wing (triangle 6) as well. Upper 3rd molars of most species have an anterior loop and at least 3 alternating triangles with a posterior portion that varies in complexity; no *Microtus* specimens show an elongated posterior extension of M3/ as in *Lemmiscus*. Only 3 closed dentine fields are present on the 3rd lower molars referred to *Microtus*. Grayson (1983) noted that the position of the mandibular foramen can be used to differentiate edentulous dentaries of *Microtus* and *Lemmiscus*. In *Microtus* this foramen is on or slightly dorsal to the ridge of bone encapsulating the posterior portion of the lower incisor and is clearly visible when the dentary is laid flat on its labial surface. In *Lemmiscus* the foramen is situated on the anterodorsal portion of this encapsulating ridge and is not distinctly visible in a direct lingual view.

Lemmiscus curtatus (Cope, 1868)

MATERIAL.—Left dentary with I, M/1–2: 7755; left dentary with I, M/1: 7794; left dentary fragment with M/1: 7828; right dentary with M/1: 7741, 7749, 7802, 7830; isolated M/1: 7735–7740, 7742–7748, 7750–7754, 7756–7793, 7795–7801, 7803–7827, 7829, 7831–7836, 7875; isolated M/3: 7895–7932; isolated M3/: 7847–7871; left edentulous dentary: 7940–7982; right edentulous dentary: 7983–8018.

DIAGNOSIS.— In living *Lemmiscus curtatus* the lower 1st molar has a posterior loop and 5 closed, alternating triangles (similar to that in Fig. 1B); a 6th triangle is present and may be broadly confluent with the anterior cap, nearly closed (Fig. 1C) or completely closed. Generally, only the labial secondary wing is well developed, although a weak lingual secondary wing may be developed. In the earliest known populations of *Lemmiscus*, the lingual primary wing (triangle 5) is widely confluent with the anterior cap (Fig. 1D; see discussion). M3/s assigned to *Lemmiscus curtatus* have an anterior loop, 2 alternating triangles, and an elongate and uncomplicated posterior loop (Repenning 1992). M/3s referred to *Lemmiscus* have 4 closed dentine fields. Edentulous dentaries were identified based on the position of the mandibular foramen (see discussion under *Microtus*, above).

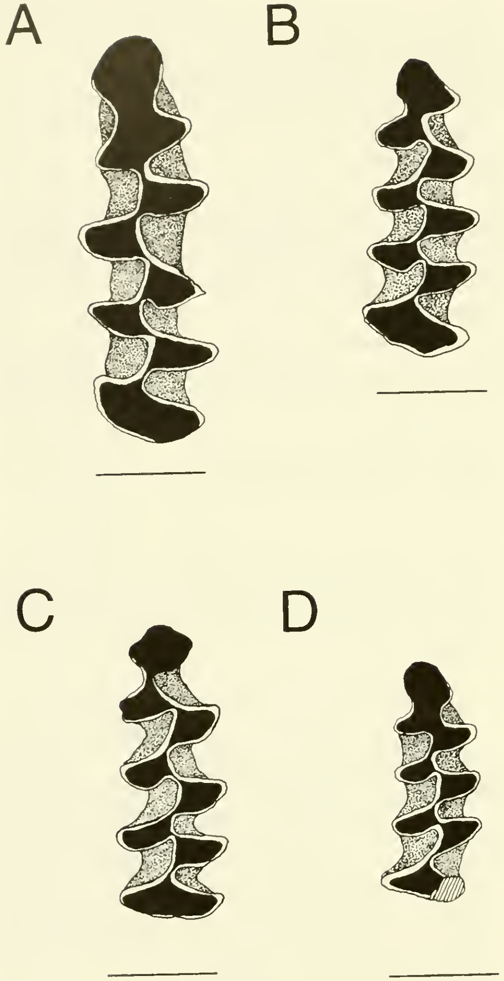

Fig. 1. Occlusal view of left M/1 of microtine rodents from Snake Creek Burial Cave: A, *Microtus* sp. (NAUQSP 7683); B, typical *Lemmiscus curtatus* morph from SCBC (NAUQSP 7738); C, a 'complex' morph of *Lemmiscus curtatus* (NAUQSP 7747) in which the 6th triangle is nearly closed; D, 4-closed triangle morph of *Lemmiscus curtatus* (NAUQSP 7734). Scale bars = 1 mm.

DISCUSSION

Today only 2 species of *Microtus* (*M. montanus* and *M. longicaudus*) are found in the central Great Basin, including the area around SCBC (Hall 1946); 2 other species (*M. pennsylvanicus* and *M. richardsoni*) presently inhabit regions bordering the Great Basin (Hall 1981). *Microtus* is reasonably well represented in late Pleistocene faunas of the Great Basin. *M. montanus* and *M. longicaudus* are usually reported as questionable identifications (see summary in Heaton 1985), but these reports appear to be based largely upon modern geographic distribution of taxa. Although 3 specimens from the Tule Springs site in southern Nevada were identified as *Microtus* cf. *M. californicus* by Mawby (1967), no discussion was provided to indicate how the identification was made, and comparisons with other *Microtus* species may not have been adequate. A single specimen from Crystal Ball Cave was tentatively identified as *M. pennsylvanicus* (Heaton 1985). Eleven M2/s (NAUQSP 8075–8085) from SCBC show distinct development of a posterolingual dentine field similar to that seen in living *M. pennsylvanicus*. Although some authors consider this feature to be unique to *M. pennsylvanicus*, it is reported to occur at least occasionally in several other species of *Microtus* (Zakrzewski 1985) and is almost universally present in *M. californicus* (personal observation). It is not known to occur in *Lemmiscus*. Until a complete survey of the development of this feature in *Microtus* species can be completed, we hesitate to refer these specimens to any given species, but note their presence in the fauna so that future considerations of this problem may take them into account. Despite its contributing little else to our knowledge of *Microtus* in the Great Basin, the material from SCBC does provide further documentation of the presence of this genus at lower elevations during the Pleistocene.

Although *Lemmiscus* is reported from numerous Pleistocene and Holocene localities outside the Great Basin (FAUNMAP Working Group 1994), surprisingly few reports have been published from within this region, where it is widespread today (Hall 1946). The earliest known occurrence in the Great Basin is in Irvingtonian (early to middle Pleistocene) deposits in Cathedral Cave, located about 40 km north of SCBC (Bell 1995). We identified *Lemmiscus* molars recovered from excavation backdirt in Smith Creek Cave (northern Snake Range) that is presumably Pleistocene in age (possibly from the reddish brown silt unit; see discussion in Mead et al. 1982). Its occurrence in the late Pleistocene was documented at Crystal Ball Cave in Utah (Heaton 1985) and Owl Cave, Nevada (Turnmire 1987); it also is known from Pleistocene-Holocene deposits in Rock Springs Cave (Jefferson et al. 1994) and from several Holocene deposits within the Great Basin (FAUNMAP Working Group 1994).

TABLE 1. Stratigraphic distribution of M/1 of *Lemmiscus* morphotypes from the 1987 excavations in SCBC. Number of specimens of each morphotype, total number of specimens, and relative percent of 4-closed triangle morphotypes are provided for each stratigraphic level. Only levels excavated in primary deposits are included. 4T = 4-closed triangle morphotype; 5T = 5-closed triangle morphotype; 6T = specimens in which a 6th triangle is well developed but not completely closed.

Stratigraphic level	# 4T *Lemmiscus*	# 5T *Lemmiscus*	# 6T *Lemmiscus*	Total # of specimens	% 4T morphotypes
3 (guano)	0	3	0	3	0
4	0	1	0	1	0
4/5	0	4	1	5	0
5	1	7	2	10	10
6	1	13	1	15	7.7
7	1	15	0	16	6.7
8	0	5	0	5	0
9	0	2	0	2	0

Most molars assigned to *Lemmiscus* from SCBC are indistinguishable from those of living *L. curtatus*, but 4 notable exceptions occur: NAUQSP 7734, 7788, 7806, and 7833 are lower 1st molars in which the lingual primary wing is widely confluent with the anterior cap (Fig. 1D). This relatively primitive morphology is not known to us to occur in living *L. curtatus*. It is the only morphology present in the SAM Cave fauna in New Mexico, with an estimated age of 875,000 yr. B.P. (Repenning 1992). Both 4- and 5-closed triangle forms are reported from the same stratigraphic levels in the Pit locality in Porcupine Cave, Colorado (a sequence dated to between 365,000 and 478,000 yr. B.P.; Wood and Barnosky 1994, Barnosky et al. 1996), and Cathedral Cave, Nevada, also considered to be Irvingtonian in age (Bell 1995). In the Pit locality the relative abundance of the 4-closed triangle forms decreases in successively younger stratigraphic levels, with a concomitant increase in relative abundance of 5-closed triangle forms (Wood and Barnosky 1994). A similar pattern was documented at the Kennewick Roadcut in Washington, where both 4- and 5-closed triangle specimens were reported (Rensberger et al. 1984, Rensberger and Barnosky 1993), with the primitive morphology found predominantly in the lower part of the section. The age of the Kennewick fauna is not precisely known, but a full review of data pertaining to the age of the Kennewick section was provided by Rensberger and Barnosky (1993), who concluded that the lowermost sections probably do not extend back into the Irvingtonian.

A total of 57 M/1s of *Lemmiscus curtatus* from the 1987 excavations in SCBC can be reliably placed in the stratigraphic sequence; of these, 3 are 4-closed triangle forms and 4 are relatively complex morphotypes in which the 6th triangle is nearly closed (Fig. 1C). Four-closed triangle specimens are evenly distributed in the middle of the stratigraphic sequence (see Table 1) but are absent from the oldest deposits; this pattern may be a result of low sample size for each stratigraphic level.

The taxonomic status of the 4-closed triangle *Lemmiscus* is uncertain, and for the present we refer these specimens to *Lemmiscus curtatus*. Specimens from SCBC represent the youngest known occurrence of this morphology and demonstrate a persistence of this form into the late Rancholabrean. The precise time of disappearance of *Lemmiscus* with this molar morphology is unknown, but its absence in the living fauna and its presence in SCBC suggest the possibility that populations of *Lemmiscus* with this morphology went extinct at the end of the Pleistocene, perhaps in response to climatic changes occurring during the glacial–Holocene interglacial transition.

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WESTERN TOAD, *BUFO BOREAS*, IN SOUTHERN UTAH: NOTES ON A SINGLE POPULATION ALONG THE EAST FORK OF THE SEVIER RIVER

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Key words: Bufo boreas, *population size, potential prey, potential predator.*

Amphibian species, including the North American western toad, *Bufo boreas*, are declining worldwide (Blaustein and Wake 1990). This decline may be related to a number of factors including human interference and habitat degradation (Blaustein and Olson 1991), indirect effects of "stress" leading to diseases such as "red-leg" (Carey 1993), mineral toxins in water that kill tadpoles (Porter and Hakanson 1976), predation on juveniles and adults (Beiswenger 1981, Olson 1989), and pathogenic fungal infections of eggs (Blaustein et al. 1994). Ross et al. (1995) summarized the status of *B. boreas* in Utah, mapped distributions of many disjunct populations, and cited evidence for possible declines in populations within the northern part of the state. These authors stressed that surveys need to be expanded and continued, especially in southern Utah, to clarify the status of these toads and to identify factors that might affect their populations.

Recent reports of *B. boreas* at 3 new montane localities (2500–3030 m elevation) in southern Utah noted adults, egg strings, and metamorphs (Ross et al. 1995). Although no exact date was given for the presence of adults and egg strings, metamorphs were reportedly observed in July at 2 of the 5 ponds surveyed earlier in the year. These are the only reports on the ecology of *B. boreas* in southern Utah. Consequently, we chose to study the natural history of a single population of *B. boreas* in this area, initially focusing on questions concerning population size and structure.

We located boreal toads at a new locality in Garfield County, Utah, along the East Fork of the Sevier River, not far from a site previously reported by Ross et al. (1995). The site is in the bottom of a long canyon with a winding, slow-moving stream whose bed is an impermeable layer of Kaiparowits clay underlain with Claron limestone. The riparian zone is dominated by the introduced Kentucky bluegrass (*Poa pratensis*) and smooth brome (*Bromus inermis*) and native wire grass (*Juncus balticus*). Present vegetation contrasts with the natural cover in the early 1900s, which consisted of various types of willows (E. L. Boshell personal communication). A weir on the east slope of the canyon creates a small pond about 30 m in diameter. Native stands of Engelmann spruce (*Picea engelmannii*) mixed with blue spruce (*P. pungens*) and Douglas-fir (*Pseudotsuga menziesii*) rise above the riparian zone. Adjacent areas were clearcut in the 1930s and later replanted with ponderosa pine (*Pinus ponderosa*). Access to the site is by an unimproved road running parallel to the stream.

We visited the study site on 23 June, 6 and 21 July, 4, 17, and 31 August, and 7 September 1996, usually from mid-morning to mid-afternoon. As we slowly walked along the main stream, its branches, and the moist slopes on either side of the road, we located toads and captured them by hand. Snout-vent length (SVL) in millimeters and weight (WT) in grams were measured for each toad before it was released at the exact point of capture. Wart patterns on the head and dark blotches on the throat and lower left leg were sketched for each individual. Suspected recaptures were later identified by comparisons with these drawings. Using the Petersen method, we estimated population size, and we tested equal catchability using a zero-truncated Poisson test (Fortran programs PETERSEN and ZERO, respectively, in Krebs 1989). Potential prey types were identified from sweeps of the vegetation using insect nets, and inferences on feeding were obtained from palpation of toad stomachs. Potential competitor and predator species were noted.

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Forty-six toads were observed; unique captures represented 35 adult toads, 17 males and 18 females. Neither tadpoles in the stream, its tributaries, or the small pond above the weir, nor newly metamorphosed toadlets or potential young-of-the-year were observed. Most toads were recorded in June ($N = 11$) and July ($N = 27$), with fewer observations in August ($N = 6$) and September ($N = 2$).

Males ($N = 16$) were smaller than females ($N = 18$) in both length and weight (ANCOVA: mean SVL for males = 86.8 mm, range 75–98 mm; mean WT for males = 64.6 g, range 52–80 g; mean SVL for females = 96.3 mm, range 81–111 mm; mean WT for females = 92.9 g, range 52–115 g; $F = 20.87$; df = 1,32; $P < .001$).

We compared the 25 non-recaptured toads observed during the first 2 visits with those 8 recaptured and 10 non-recaptured toads observed during the last 5 visits to estimate population size. The Petersen estimate, with replacement, was 53 adult toads (95% CL = 38–99). A goodness-of-fit test of observed and expected values for the zero-truncated Poisson test of equal catchability could not reject the null hypothesis ($\chi^2 = 1.21$; df = 3, $P > 0.8$).

A null hypothesis, no difference between male ($N = 4$) and female ($N = 6$) growth in mm/day, was accepted (Mann-Whitney test, $U = 4.0$, $Z = 1.7$, 2-tailed P value = 0.09). Combined recaptures for males and females allowed an average estimate of 0.17 mm/day (95% CL = 0.09–0.25) growth in SVL during the study period.

We swept five 10-m transects with a 40-cm-diameter insect net in the vicinity of captured toads. The 169 arthropods caught in these sweeps represented 7 orders: Homoptera (27%), Coleoptera (25%), Diptera (18%), Orthoptera (17%), Hymenoptera (8%), Hemiptera (4%), and Arachnida (1%). Orthopterans ($N = 29$) had much larger average body lengths (20.1 mm, 95% CL = 18.7–21.5) than those ($N = 140$) of all other taxa (2.8 mm, 95% CL = 2.4–3.1). All toad stomachs examined by palpation in July and early August contained large prey (>2.8 mm).

Two dead adult toads were found under a clump of dried grass in a burrow also occupied by 4 live juvenile northern water shrews (*Sorex palustris*). Although we examined the partially dried carcasses, we could not determine that the toads were killed by shrews, although it is suspected that shrews were feeding on them (Fig. 1). Numerous wandering garter snakes (*Thamnophis elegans vagrans*) were observed in the area. All were too small (SVL < 0.5 m) to swallow any of the toads we measured, although they could definitely prey on juveniles and tadpoles. The only other amphibian species observed at the study site was the leopard frog, *Rana pipiens*, whose numbers appeared fewer than *B. boreas* (only 6 were observed during the study period).

A population of *B. boreas* in southern Utah, studied during summer 1996, contained only large, presumably old adults, with no indication of size-age structure that would suggest juvenile recruitment. The estimated population size of 53 adults is based on individuals that were recaptured at random; however, sample sizes were uneven for the period of study, and this number relies on the assumption that grouping data into 2 samples does not bias the true estimate of population size. We also assumed no recruitment from migration of adult toads into or out of the study area because of the widely separated populations in this area. Growth rates estimated from a very small sample of recaptures over a relatively short period of time probably do not accurately reflect annual growth rates. A femur from 10 concentric layers of bone in each osteon may indicate an old adult toad. However, sections of bone from toads of various sizes are needed to verify this notion. Toads were not observed feeding, but their stomachs appeared to contain large insects (possibly orthopterans). Because grasshoppers are the largest but not most abundant potential prey, toads may be selectively feeding on them. Dead toads can be eaten by shrews, but whether shrews kill toads is not known. Numerous wandering garter snakes may prey on tadpoles and small toads but are too small to swallow adult toads in this population. There appear to be few, if any, competitors to *B. boreas* for food and habitat space. *R. pipiens* and *B. boreas* occur together along the water courses, perhaps suggesting that critical resources for

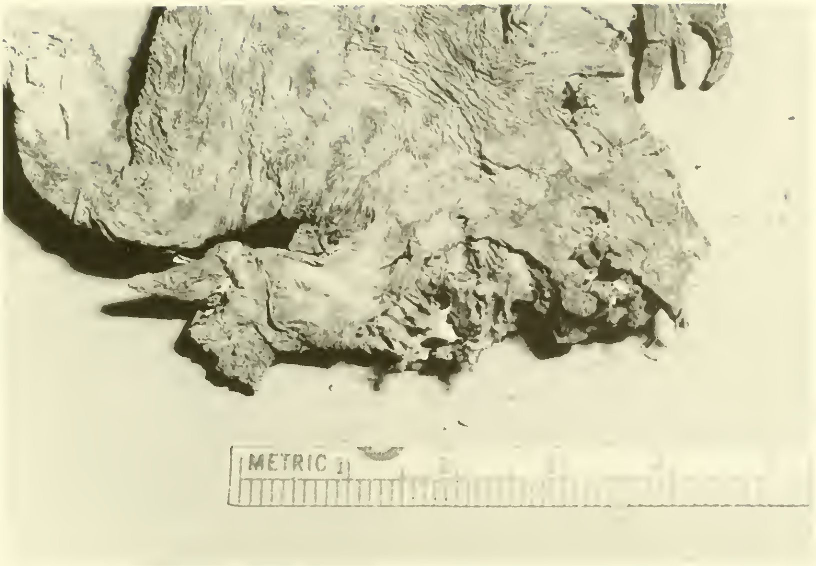

Fig. 1. Venter of a dead western toad (*Bufo boreas*) found in the burrow of a northern water shrew (*Sorex palustris*) in southern Utah; note the jagged, apparently chewed edge near the head end of the dried carcass.

survival are either different for both species or, if similar, are not limiting.

Toads appear to be clumped along water courses or in wet seepage areas with abundant grasses and sedges, habitat similar to those previously described for the species in other areas (e.g., Campbell 1970). From previous descriptions by Black and Brunson (1971), the pond above the weir at this study site appears ideal for breeding aggregations of toads.

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WESTERN WOOD-PEWEES ACCEPT COWBIRD EGGS

David R. Curson[1], Christopher B. Goguen[1], and Nancy E. Mathews[1]

Key words: Western Wood-Pewee, Contopus sordidulus, *brood parasitism, Brown-headed Cowbird,* Molothrus ater, *accepter.*

The Western Wood-Pewee (*Contopus sordidulus*) is an infrequently recorded host of the brood parasitic Brown-headed Cowbird (Friedmann et al. 1977, Friedmann and Kiff 1985), as are the majority of tyrannid flycatchers (Petit in press). A minority of cowbird host species, termed rejecters (Rothstein 1975), reject cowbird eggs by ejecting them from the nest, burying them in the nest bottom, or deserting the parasitized nest. Hosts that do not exhibit this response to parasitism are called accepters. Hosts tend to either accept or reject in a consistent manner (Rothstein 1975; but see Petit 1988, Goguen and Mathews 1996). A species can be assumed to be an accepter if parasitism is noted in more than 20% of its nests (Friedmann et al. 1977). Studies may underestimate the frequency of parasitism of rarely used hosts, if these hosts are rejecters, because cowbird eggs may be ejected before being observed. The status of these hosts can be ascertained correctly only by experimentation.

Relatively few tyrannid flycatcher species have been tested in this regard. Eastern Kingbirds (*Tyrannus tyrannus*) and Western Kingbirds (*T. verticalis*) are rejecters (Rothstein 1975), while Eastern Phoebes (*Sayornis phoebe*) and Least Flycatchers (*Empidonax minimus*) are accepters (Rothstein 1986, Briskie and Sealy 1987). We report experiments that demonstrate the Western Wood-Pewee is an accepter species.

The study site is in pinyon pine–one-seed juniper (*Pinus edulis–Juniperus monosperma*) woodlands in Colfax County, northeastern New Mexico. Between 1992 and 1996 we located and monitored nests of Western Wood-Pewee as part of a study of the nesting dynamics of the pinyon-juniper avian community. We experimentally parasitized 10 nests during 1995 and 1996 to determine the accepter status of Western Wood-Pewees at this site. A single fresh Brown-headed Cowbird egg was added to each nest, and no host eggs were removed. Eggs were added during daylight hours at the following stages of the nest cycle: nest-building (3 nests), egg-laying (4 nests), or early in incubation (3 nests). Some nests were observed for 30 min after the egg was added to record the adult pewee's response to the introduced egg. We considered the egg accepted if it remained in the nest, with adult pewees attending, for 4 d.

At unmanipulated Western Wood-Pewee nests we recorded a parasitism frequency of 16% (16 of 101 nests). Two nests were parasitized multiply, each with 2 cowbird eggs. Cowbird eggs were accepted for at least 4 d in 13 nests, hatched in 7 nests, and fledged in 3 nests. No nest fledged both a cowbird and a pewee or more than a single cowbird. At 1 nest pewees accepted a cowbird egg after an adult had physically attacked the female cowbird when it first removed a pewee egg and when it parasitized the nest 2 min later. We noted 2 cases of possible cowbird egg rejection, 1 involving ejection and the other desertion. In the former case the cowbird egg was laid in an empty nest and disappeared before the 1st pewee egg was laid. In the latter case a nest was deserted during incubation, following parasitism and clutch reduction from 3 pewee eggs to 1 pewee egg and 1 cowbird egg.

Pewees accepted the cowbird egg at 8 of 10 (80%) experimentally parasitized nests. Eggs accepted by pewees remained in nests between 4 and 19 d prior to being depredated along with the pewee's clutch, being removed by a human observer, or hatching (1 nest). At the nest where the cowbird hatched, the nestling fledged successfully. The immediate response of a pewee returning to a freshly "parasitized" nest, during incubation, was noted at 1 nest. This bird perched on the nest rim, looked briefly into the nest, and settled down to incubate, showing no sign of having noticed any change in its nest.

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Cowbird eggs disappeared within 4 d at 2 experimentally parasitized nests. At a nest tested near the end of nest-building, the cowbird egg disappeared within 2 d and the pewee's clutch was initiated 4 d later. At another nest, tested during egg-laying, we found the cowbird egg beneath the nest when we next visited it 4 d later; the pewee clutch had increased from 2 to 3 eggs. A 2nd cowbird egg, added upon discovery of this ejection, was found under the nest after 3 d, while the pewee clutch remained intact.

The acceptance of experimentally added cowbird eggs at 8 of 10 nests demonstrates that the Western Wood-Pewee, like other small tyrannids tested so far, is a cowbird egg accepter (Rothstein 1975). The observed desertion of an unmanipulated nest may have resulted from partial clutch reduction rather than parasitism, and thus probably does not represent true cowbird egg rejection. Experiments have shown at least 2 other accepter species, Eastern Phoebe (Rothstein 1986) and Clay-colored Sparrow (*Spizella pallida;* Hill and Sealy 1994), to desert nests in response to partial clutch reduction but not parasitism per se.

The disappearance of the experimental cowbird egg from a nest tested during the building stage may have simply represented a generalized response to any object found in the nest prior to the host's egg-laying rather than a response specific to brood parasitism (Rothstein 1975). The Least Flycatcher, an accepter, rejected cowbird eggs that were experimentally introduced to 2 nests at the building stage, but did so by nest desertion (Briskie and Sealy 1987). Furthermore, nest predation, or removal of the egg by a cowbird, cannot be ruled out.

However, the experiments did elicit an instance of true cowbird egg rejection. The repeated ejection of a cowbird egg from a nest containing a host clutch provides circumstantial evidence that pewees possess the behavioral and physical traits required to reject. Considering the obvious selective advantage of such behavior, it is surprising that cowbird egg ejection is not more widespread, or even fixed, in the pewee population.

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BOOK REVIEW

Few and Far Between: Moments in the North American Desert. John Martin Campbell. Museum of New Mexico Press, Santa Fe, NM. 1997. $29.95 paperbound, $40.00 clothbound.

By its title and theme, *Few and Far Between* could be intended as a scholarly book of science. After all, the study of deserts is science, and archeology and anthropology are forms of science. Photographs, too, can introduce one to science when presented accurately and factually. However, to one who has been trained academically about the deserts of North America (and who has trained others), to one who has lived in the deserts for a lifetime, the book presents a pictorial introduction to deserts for someone who is not trained in science. There is little in the book of scientific worth. Furthermore, it contains too many errors to be of much value to a scientist, but even the reader with limited knowledge of science should be presented with accurate information.

The book consists of the author's photographs with captions and minimal discussions. In addition, one of the illustrations is a map of part of western North America showing the 4 different deserts of the continent, or presenting the "one desert" which the author repeatedly uses in his writing. The photographs, primarily studies in blacks, grays, and white, with a few in color, are the fundamental contributions to the publication. The written part of the volume is limited. From Tony Hillerman's foreword and Campbell's preface, it presents 3 sections—"Origins," "The Face of the Desert," and "Desert People"—concluding with an extensive though incomplete bibliography. The Museum of New Mexico Press is commended for the clean copy and reproduction of photographs and Campbell is complimented for his talents as a photographer, even those pictures not directly of the desert. He is criticized for the many errors found in the book and for using technical information without documentation.

The author has been described as an archeologist, anthropologist, photographer, and renaissance writer, and the book reveals all of those characteristics.

Perhaps only the author knows the meaning to the title *Few and Far Between.* It certainly cannot refer to the animals that are discussed in the book, because animals are common in deserts. It might refer to the scarcity of trees or other perennial plants because many of the photographs depict these organisms, but it couldn't mean plants in general. Deserts are covered with ephemerals and other forbs when physical conditions are optimal.

The 14 color photographs are a part of the introduction to each of the 3 sections, and the 59 black-and-white photographs each occupy a full page accompanied by descriptive information on a facing page. This information is limited to 1 or 2 paragraphs, usually less than half a page. About half of these black-and-white photographs are in the section entitled "The Face of the Desert." While the book is about the desert, not all photographs are appropriate to the desert. Photographs not related to the desert are marginally appropriate or totally inappropriate to the book's title and main theme.

From a scientist's perspective there are several objections to the book's thesis. One is the repetitive reference to the "North American Desert" as a single geographic area. This is noted in the subtitle to the book and is repeated throughout the writing. The "Origins" section, page 2, contains a brief description of all Earth's deserts. The statement is made that the "North American [desert] is fifth in size," further suggesting there is a single desert. Science recognizes both physiographically and biologically 4 very different geographic areas and 4 unique deserts. Additionally, smaller regions such as eastern Washington and eastern Utah are desert, but decidedly not a part of the specific desert claimed by Campbell.

One common entity is found in all these different deserts—the lack of adequate water throughout most of the year. However, this is only 1 reason for a region to be designated as desert. Other physical features include location of mountain ranges and direction of prevailing winds. Some of this is explained in Campbell's introductory statements.

In his discussion of deserts on the different continents, Campbell almost apologetically includes the Arctic and Antarctic regions in his statement that "30 percent of the earth's land surface is covered by desert." The Arctic and Antarctic regions are, in fact, extremely cold deserts because water is not readily available to support life. However, the book is about the deserts of North America and, while illustrations of the Antarctica "desert" would be inappropriate, photographs of the Arctic region of North America would have made the book more complete. If one would read in some 19th-century historical writings of North America, a reference would be found to the "Great American Desert" of central North America, extending from Mexico into Canada. This extensive geographic region, now referred to as the grasslands biome of the continent, is no longer described as desert. However, it may be considered as appropriate an example of a desert as some of those written about and shown by Campbell. This Great American Desert might also have been included as a part of the "North American Desert" presented by the author.

Another objection to Campbell's presentation in photograph and dialogue is the idea that the Great Basin Desert is found north and east of its actual physiographic boundaries (map on page xii). Admittedly, these extended regions are desert, but they cannot be correctly defined as Great Basin. Excluding the Arctic, the 4 primary deserts of North America are detailed in this map. Campbell's map shows both the Great Basin Desert and the Mojave Desert incorrectly. The Great Basin Desert, for instance, does not extend northward into the state of Washington, nor eastward into central and southern Wyoming, nor into eastern Utah, nor into northwestern or southwestern Colorado. It certainly does not extend into northeastern Arizona nor into New Mexico. The Great Basin Desert conforms to the area covered by the Basin and Range Province and is more restricted in geographic area. (References: *Physiography of Western United States*, Nevin M. Fenneman, McGraw-Hill Book Company, 1931; *Natural Regions of the United States and Canada*, Charles B. Hunt, W.H. Freeman and Company, 1974; *Exploring the Great Basin*, Gloria Griffen Cline, University of Oklahoma Press, 1963; *The Trees and Shrubs of the Southwestern Deserts*, Lyman Benson and Robert A. Darrow, University of Arizona Press and University of New Mexico Press, 1954; *Deserts*, James A. MacMahon, Alfred A. Knopf, 1985, this latter being one of The Audubon Society Nature Guides and the only reference of these 5 included in Campbell's bibliography.)

Campbell's map is also incorrect for the Mojave Desert. One of the important evidences of this desert is the *Larrea/Ambrosia* shrub association which extends into southwestern Washington County of Utah, into northwestern Mohave County of Arizona (both areas are shown on the map incorrectly as being Great Basin Desert), and along the Colorado River farther south than shown by Campbell's map.

The book contains many errors and inconsistencies in writing. On page 4 the caption to the color photograph uses the binomial of the arrowweed as *Pulchea servicea*. The correct scientific name of this shrub is *Pulchea sericea*.

A statement is made on page 6 that the desert "encompasses all of Nevada," which statement is in error. High mountains, certainly at elevations immediately below timberline on the northern slopes, are not desert, even though they are surrounded by desert. These high mountains are sometimes referred to as "islands in the sky," but these islands are not part of the desert. A statement is made on page 50 about "the various desert mountains," with a specific reference to "elevations of from more than nine thousand feet to more than fourteen thousand feet above sea level." This is implied by Campbell to be desert.

On page 16 the author states that "the rain forests of the Northwest Coast, [are] the only true jungles of any temperate-zone region on earth." This is not true of all such regions on Earth, but why is this even considered in a discussion on deserts? On unnumbered page 45 is the sentence, "Not a single major desert plant species of the Mexican state of Sonora, for example, grows in the desert of Washington." With the great difference in latitudes (Sonora 30°N, Washington 45°N), how could anyone knowledgeable of plants expect them to be similar in these geographically separated areas? Campbell reverts to the 19th- and early 20th-century reference to the "life zones of C. Hart Merriam" instead of using the now scientifically acceptable biomes idea.

On page 50 an incorrect statement is made that the "sage grouse is exclusive to the Great Basin." The known distribution of the Sage Grouse extends into southern Canada and central North America, far beyond the reaches of the Great Basin. Also on page 50 is a reference to "pronghorn antelope." This mammal is admittedly a pronghorn, but it is assuredly not an antelope even though the once-popular song refers to "where the deer and the antelope play."

On page 52 is the statement that "the Great Basin Desert grows relatively few plant species." The plant species may be few in number compared to a tropical rain forest, perhaps, but a great variety of forbs and annuals are found in all North American deserts.

Reference to the creosotebush (this should be 2 words, not 1) occurs on pages 53 and 54, with the statement that "each . . . parent root may produce dozens of bushes over thousands of square feet of desert floor." The creosote bush does clone to produce other plants over time and over limited areas, but over "thousands of square feet" is an exaggeration.

The full-color illustration on page 55 is of the purple prickly pear (*Opuntia violacea*). According to N.L. Britton and J.N. Rose (*The Cactaceae*, Volume I, page 144), this scientific name is questionable. These authors explain that this plant "can never be critically identified" because it was described from drawings brought back from the Southwest and not from actual specimens.

It is stated on page 56 that "the Sonoran [Desert] runs right down to the sea" and "it has its equally unique shore fauna, including great sea turtles." How can an animal, such as a sea turtle, that spends its entire life in the ocean, except for brief moments on land for oviposition, be referred to as a desert animal?

The photo and narrative on page 58 and unnumbered page 59 claim that "arroyos result . . . from the absence of close-growing vegetation." This appears to be quite true about the one pictured in New Mexico, but there are countless examples throughout the American Southwest where arroyos do produce diverse species and large numbers of plants.

The caption to the photo on unnumbered page 61 is "storm on San Rafael Reef." This photo shows clouds, but no storm. Similarly, that on page 62 and unnumbered page 63 is "cloudburst on the Red Desert" without any evidence of water.

Ground temperatures are discussed on page 64 with the note that they "have reached a staggering 190 degrees F." In the opinion of the writer of this review, documentation of this temperature should be included. Another inconsistency is found on page 72 in reference to the photo of a playa. The statement is made that the floor of a playa may be "as flat as a tabletop and as solid as a rock." There is no objection to the statement, but the playa shown is fractured with mud cracks and is anything but flat and certainly not solid because of these cracks. On page 74 a statement is made that quagmires are "bottomless." Perhaps this is included as a form of poetic expression, but quagmires are not really bottomless.

A "north country prickly pear" is shown and discussed on page 90 and unnumbered page 91. In reference to fruit size, the expression is used that "desert prickly pears bear fruit two inches long; others, as with those of this little northernmost species, are as big as thimbles." Compared to 2 inches, a thimble should be referred to as small rather than big. Is there such a thing as a 2-inch thimble?

Swallows' nests are shown on unnumbered page 107 with the name of the Cliff Swallow given as *Hirundo pyrrhonota* on the facing page. The genus name for this bird is *Petrochelidon*, not *Hirundo*.

A statement is made on page 112 that the Joshua tree "nearly exclusively belongs to the Mojave [Desert]." The map on page xii shows the Mojave Desert scarcely in Arizona where Joshua trees are common and not at all in southwestern Utah where they are abundant. The word "nearly" probably justifies these inclusions.

In the narrative on page 116 the first paragraph is about the accompanying picture of a Mexican blue palm. The binomial used for the plant, however, is a synonym and not the accepted scientific name. The second paragraph about the Cochimi Indians has no recognizable reference to the picture of the palm.

The logical explanation might be that this second paragraph introduces "Desert People," which is the last section of the book beginning on the next page.

The caption to the color photograph on page 120 is about the prickly pear cactus as a food source. The photograph, however, shows a tree cholla, not a prickly pear cactus.

The discussion on page 121 is about "rabbit drives." The author then states that "fifteen or more species of other rodents were eaten" (emphasis added). This statement suggests that rabbits are rodents.

According to the information on page 127, "Chaco Canyon lies squarely in a Great Basin Desert environment." As stated previously in this review, New Mexico is not in the Great Basin, although the environment may be somewhat similar, and certainly the area in and around Chaco Canyon is suggestive of desert.

The photo on unnumbered page 136, showing a salmon fisher's roost in Wasco County, Oregon, is interesting historically, but the Columbia River and its tributaries are definitely not in any desert. Like so many other references, some of which are stated in this book review, Duchesne County, Utah (reference page 144), is not even remotely near a desert.

Despite these technical criticisms, the reader of *Few and Far Between* should be entertained by the writing, especially such poetic expressions as "I got to go along" (page x), "desertic Pacific coast" (page 16), the "poisoned water to boot" (page 20), the "honest river" and the "exotic rivers" (page 68). On the other hand, the reader may find it monotonous with some of the redundancies that occur.

Campbell may have been more at peace with his science readers had the draft been more carefully critiqued and edited by a competent scientist, and had the author and editors paid more attention to detail and documentation of what supposedly is fact. *Few and Far Between* is obviously not intended for the scientist, but it is a photographer's contribution showing his ability to record in that medium.

Andrew H. Barnum
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CHIRONOMIDAE (DIPTERA) OF THE COLORADO RIVER, GRAND CANYON, ARIZONA, USA, I: SYSTEMATICS AND ECOLOGY

James E. Sublette[1], Lawrence E. Stevens[2], and Joseph P. Shannon[3]

ABSTRACT.—We describe the chironomid midge fauna of the Colorado River between Glen Canyon Dam and Lake Mead, Arizona. This depauperate fauna, consisting of 38 species, is dominated by euryecious Nearctic or Holarctic orthocladine taxa. In addition, a small Neotropical faunal component is represented by *Polypedilum obelos* Sublette & Sasa and *Rheotanytarsus hamatus* Sublette & Sasa.

The following new synonyms are given: *Protenthes riparius* Malloch 1915 with *Tanypus bellus* Loew 1866 [=*Procladius* (*Psilotanypus*) *bellus* (Loew)]; *Cricotopus olivetus* Boesel 1983 with *Cricotopus* (*Cricotopus*) *annulator* (Goetghebuer) 1927; *Cricotopus edurus* Sublette & Sublette 1971 with *Orthocladius infuscatus* Malloch 1915 [=*Cricotopus* (*Cricotopus*) *infuscatus* (Malloch)]; *Cricotopus subfuscus* Sublette & Sublette 1971 with *Orthocladius infuscatus* Malloch 1915 [= *Cricotopus* (*Cricotopus*) *infuscatus* (Malloch)]. The following new species are described: *Cricotopus* (*Cricotopus*) *blinni* Sublette, *Cricotopus* (*Cricotopus*) *herrmanni* Sublette, *Metriocnemus stevensi* Sublette, and *Cladotanytarsus marki* Sublette. We discuss the distribution and ecology of each chironomid species collected in this large, regulated, aridlands river.

Key words: Chironomidae, Colorado River, distribution, euryecious species, Glen Canyon Dam, Grand Canyon, midges, new species, synonymies.

Although chironomid midges are often numerically dominant aquatic macroinvertebrates in large river ecosystems, relatively few taxonomic studies have been conducted in the American West. The known distributions of chironomids in western North America are principally based on individual species records in various works and on comprehensive studies by Sublette (1960, 1964) and Sublette and Sublette (1979). Sublette and Sublette (1979) report on material from headwater reaches of the Colorado River in the upper San Juan and Gila drainages of New Mexico. Cowley (1995) examines the chironomid fauna of the upper Rio Grande, and Ruse et al. (unpublished data) identify several chironomid species in the headwaters of the Arkansas River in Colorado; both studies report species that also occur in the Colorado River. Wolz and Shiozawa (1995) identify chironomid genera of the upper Green River in low-velocity habitats at the Ouray National Wildlife Refuge, Utah, and relate flow

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velocity to assemblage structure. Spindler (1996) reports on chironomid distribution in 10 tributaries in Grand Canyon. Also, Pearson (1967) and Rader and Ward (1988) describe the invertebrate fauna of the Green River near Flaming Gorge Dam and in the upper Colorado River, respectively.

Chironomid midges are abundant in the Colorado River in Grand Canyon (Leibfried and Blinn 1986, Blinn et al. 1992, Stevens et al. 1997). This is the largest river in the American Southwest, flowing 2250 km from the Rocky Mountains to the Sea of Cortez, and it is heavily regulated by numerous diversions and impoundments (Hirsch et al. 1990). However, no study of chironomid taxonomy has been conducted in Grand Canyon.

In this paper we describe and review the taxonomy and ecology of chironomid species in the Colorado River between Glen Canyon Dam and Lake Mead, including the entire Grand Canyon section of the river. Because our collections are primarily from the mainstream corridor, additional collecting in tributary streams, springs, and seeps will greatly increase the number of species recognized in Grand Canyon (cf. Spindler 1996).

METHODS AND MATERIALS

Study Area

The Colorado River flows 475 km from the base of Glen Canyon Dam (975 m elevation) to Lake Mead (350 m elevation) through Sonoran and Mojave Desert terrain, through lower Glen Canyon and all of Grand Canyon (Turner and Karpiscak 1980; Fig. 1). By convention, locations along the Colorado River are designated in river miles from Lees Ferry. The river passes through 13 bedrock-defined geomorphic reaches, and the Paria (km 1) and Little Colorado (km 98) rivers create 3 turbidity segments (Schmidt and Graf 1990, Stevens et al. 1997).

Field Methods

Adult and pharate aquatic Chironomidae were collected throughout the year in 1976–77 and 1990–91 by sweep-netting riparian vegetation (mostly *Salix exigua* Nutt., *Tamarix ramosissima* Loureiro, and *Baccharis* spp.), white and UV light-trapping, dip-netting, and larval rearing from benthic spot and quantitative samples (Stevens et al. 1997).

Taxonomy

Taxonomic determinations and descriptions were made by J.E. Sublette. Specimens from Grand Canyon which are new to science, and which also occur in other river systems, have been included in the type series of the new species described here. Some adult specimens that had been collected by sweep-netting may be associated with tributaries or springs; however, many individual larvae collected from the river were reared to emergence for identification.

Most of the morphological terminology used here follows Sæther (1980); however, in the Orthocladiinae the genitalia appendages were named by position rather than homology inferred by Sæther (1980). We term the superior volsella the basimedian gonocoxite lobe, and the inferior volsella is here referred to as the basidorsal and basiventral gonocoxite lobes. We followed Sæther's terminology for Chironominae genitalia. The terms *bacatiform papillae* and *nasiform tubercles* for structures on the pupal wing sheath are employed for *perlen* and *nasen*, respectively (Sublette and Sasa 1994). The basal palpomere of adult chironomids is weakly chitinized and frequently partially collapsed; consequently, only measurements for the apical 4 palpomeres are given. The term *temporal setae* here includes both the postorbital and outer vertical setae. If the frontal setae are continuous with temporals, they are also included. The length ratio of the gonocoxite to the gonostylus is given as Gc/Gs; gonocoxite length is measured along the ventral midline of the gonocoxite. In the pupa the anal lobe ratio (ALR; Soponis 1977) is the length of the longest anal macroseta divided by the anal lobe length. Ventral head length of the larva is measured from the medial apex of the mentum to the outer edge of the occipital ring.

In descriptions of new species, morphometric and meristic features of the holotype male are listed first, with the range of variation for paratypes and the number upon which the statistic is based provided parenthetically unless the holotype was unique. In other species descriptions the range is given with the number of specimens upon which the statistic is based, listed in parentheses immediately following.

The original citation is given in each species description, along with references to subsequent studies of that species. If a species has

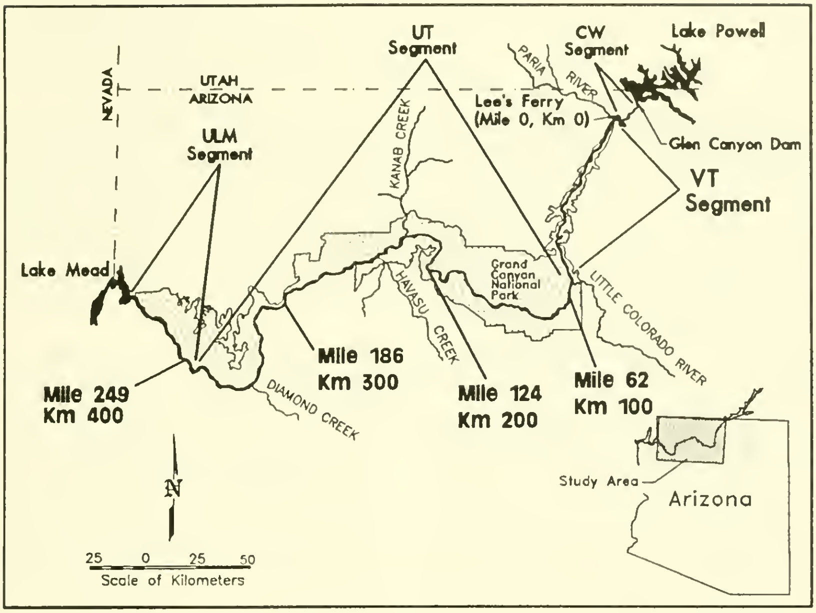

UT Segment
CW Segment
Lake Powell
UTAH
ARIZONA
NEVADA
PARIA RIVER
KANAB CREEK
Lee's Ferry (Mile 0, Km 0)
Glen Canyon Dam
ULM Segment
VT Segment
Lake Mead
Grand Canyon National Park
HAVASU CREEK
LITTLE COLORADO RIVER
Mile 186 Km 300
Mile 249 Km 400
DIAMOND CREEK
Mile 124 Km 200
Mile 62 Km 100
Study Area
Arizona
N
25 0 25 50
Scale of Kilometers

Fig. 1. Map of the study area between Lake Powell and Lake Mead, Arizona, showing 13 geomorphic reaches (Schmidt and Graf 1990) and 3 turbidity segments (Stevens et al. 1997): CW = clearwater segment, VT = variably turbid segment, and UT = usually turbid segment. Also shown is upper Lake Mead (ULM), a usually turbid, lacustrine segment.

been reviewed or revised, literature listed in that study is not included.

Deposition of type material is indicated by the following abbreviations: California Academy of Science, CAS; United States National Museum of Natural History, USNM; Academy of Natural Sciences of Philadelphia, ANSP; Illinois Natural History Survey, INHS; American Entomological Institute, AEI; University of California–Riverside, UCR; University of Colorado, U of C; University of Minnesota, UMN; Brigham Young University, BYU; James E. Sublette collection, JES; Scott J. Herrmann collection, SJH. Non-type material collected in Grand Canyon, unless otherwise indicated, is retained at Northern Arizona University.

Ecology

We review existing information on the ecology of North American Chironomidae and provide some additional data from our collections. In those cases where a species has a Holarctic distribution, selected reference to the European literature is made. Two regional biotic indices have been developed in North America, based on water quality and chironomid distribution. The North Carolina biotic index (NCBI; Lenat 1993) references Hilsenhoff's Wisconsin biotic index (Hilsenhoff 1977, 1982, 1987, 1988); therefore, only the NCBI is cited here. The NCBI, based on larvae from macrobenthic samples, lists only species groups because the taxonomy of non-adult chironomids is less definitive. The NCBI is based on a range of 0–10, with 0 being the most intolerant to pollution and 10 the most tolerant. As Lenat (1993) indicates, comparisons between different geographic regions may be uncertain; nevertheless, because citation of ecological tolerances from other regions may have value for broad-ranging species, it is provided here.

TAXONOMIC DESCRIPTIONS

Subfamily Tanypodinae

Procladius (Psilotanypus) bellus (Loew)

Tanypus bellus Loew 1866:4; type locality, D.C.

Protenthes riparius Malloch 1915:389; type locality, Thompson's Lake, Havana, IL. *New synonym.*

Procladius riparius (Malloch); Roback 1971:167, holotype male.

Procladius bellus (Loew); Kowalyk 1985:88, larval morphology.

Procladius (Psilotanypus) bellus (Loew); Roback 1971: 162, revision, synonymy, adults; 1980:31, larva and pupa; Sublette and Sublette 1979:61, in list; Parkin and Stahl 1981:122 and Stahl 1986:70, ecology; Hudson et al. 1990:5, in list; Oliver et al. 1990:15, in catalog; Epler 1995:3.54, larva.

DIAGNOSIS.—Adults: Keyed from other members of the Nearctic fauna by Roback (1971); larva and pupa keyed by Roback (1980). Adults range from almost black (early season collections or at higher elevations or latitudes) to pale yellow with pale orange-brown vittae.

DISCUSSION.—*Procladius riparius*, here synonymized with *P. bellus*, is a typical dark form except for genitalia (Roback 1971). Examination of specimens from within the range of Malloch's original material suggests that pinned specimens and genitalia mounts were mixed, with the genitalia nominally associated with the pinned holotype of *P. riparius* actually being that of *Coelotanypus concinnus* (Coquillett). Both species occur in central U.S. and, presumably, the specimens were inadvertently switched when slides from the collection were mounted. Malloch's presumptive holotype *P. riparius* genitalia were illustrated by Roback (1971: Figs. 254, 255) with a double megaseta, a condition that has been observed frequently in *C. concinnus* but not in species of *Procladius (Psilotanypus)*. Roback (1971) synonymized the paratypes of *P. riparius* but not the holotype, because of the peculiar genitalia.

ECOLOGY.—Typically, *P. bellus* occurs in the littoral zone of lakes and reservoirs (Sublette 1957, Rosenberg et al. 1984) or other shallow lentic water (Wrubleski 1987, Wrubleski and Rosenberg 1990), in slow-moving streams, and along backwater areas of faster moving streams. It was uncommon in a Laurentian stream system, occurring in quiet water on finer sediments with vegetation (Cloutier and Harper 1978), and rare, comprising only 0.4% of Tanypodinae males/m^2/yr, in a brown-water stream in Alberta (Boerger 1981). Ferrington and Crisp (1989) reported that this species is characteristic of the recovery region below enrichment zones produced by wastewater treatment plant effluents in 2 small streams in Kansas. In the upper Arkansas River, Colorado, adults were taken at 1444–1618 m elevation (Ruse et al. unpublished data). The single Grand Canyon specimen was collected near the inflow into Lake Mead during high lake level.

DISTRIBUTION.—Widely distributed in North America.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 269.5, 365 m elev.

SUBFAMILY DIAMESINAE

Diamesa heteropus (Coquillett)

(Figs. 2–5)

Tanypus heteropus Coquillett 1905:66; type localities, Washington, New Mexico, and New Hampshire (Hansen and Cook [1976] suggest the type series was mixed).

Diamesa heteropus (Coquillett); Hansen and Cook 1976:95, revision, synonymy, distribution; Sublette and Sublette 1979:64, in list; Ferrington 1983:106, distribution; Herrmann et al. 1987:321, distribution; Oliver et al. 1990:17, in catalog.

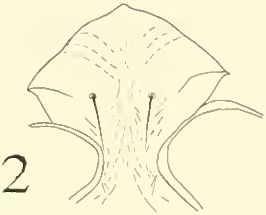
PUPA.—The pupa has been known previously (Hansen and Cook 1976) but not described. Exuviae entirely pale brown to dark brown. Abdomen length 3.32–6.11 mm.

Cephalothorax: Large frontal setae present on the frontal apotome (Fig. 2); length 139–281 µm. Thoracic horn (Fig. 3), length 359–515 µm. Median suture with moderate tubercles on either side. Precorneal setae 2, of unequal length, with the longer being 139–281 µm. Dorsocentrals 3, small, almost in a line, with the anterior seta being largest. Wing sheaths without bacatiform papillae or nasiform tubercles.

Abdomen: Spine pattern (Fig. 4). Anal lobe (Fig. 5); anal macrosetae length 289–372 µm; ALR 0.79–0.84.

DIAGNOSIS AND DISCUSSION.—The combination of hairy eyes, plumose antenna, and distinctive genitalia (Hansen and Cook 1976: Fig. 113) serves to differentiate the male. The pupal armature (Fig. 4) appears distinctive among western *Diamesa*. Tergal and sternal spines are similar to those of *Diamesa incallida* (Walker) (cf. Sæther 1969: Fig. 13, as *Diamesa fonticola* Sæther), but that species lacks the well-developed spines on tergum II of *D. heteropus*. The *Diamesa haydaki* Hansen pupa (previously undescribed) has a similar armature, but the sternal spines are more slender and are dark to the base (best observed on T V–VII).

ECOLOGY.—*Diamesa heteropus*, the most common species of *Diamesa* in western North America, inhabits cool to cold streams, including spring runs, on cobble-gravel-sand bottoms. In the upper Arkansas River of Colorado it has been taken from near the headwaters to Pueblo Reservoir at elevations of 1431–2905 m (Ruse et al. unpublished data). In New Mexico it is widely distributed below elevations of 2000 m, usually emerging from September through March (Sublette and Sublette 1979).



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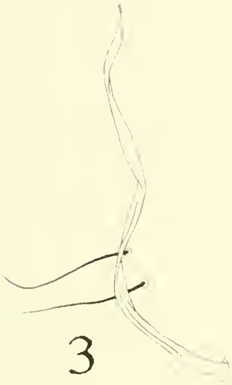

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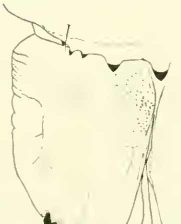

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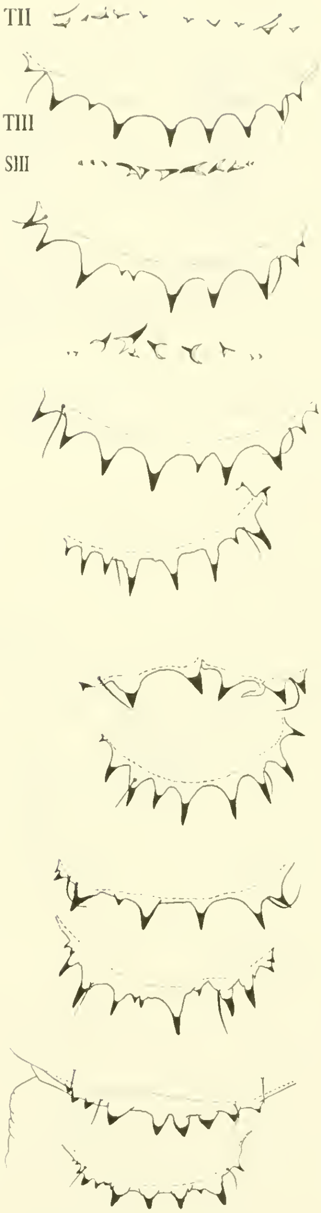

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Figs. 2–5. *Diamesa heteropus.* Pupa: 2, frontal apotome; 3, respiratory horn; 4, abdominal spine pattern (the T IV/S IV–T VIII/S VIII spine sets are shown sequentially); 5, anal lobe.

The species is rare in Grand Canyon, probably due to the lack of suitable substrata throughout much of the canyon.

DISTRIBUTION.—Alaska to Minnesota, south to California and New Mexico.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 specimen from river mi 61.0, 840 m elev. Reared material from New Mexico and Colorado was also examined.

SUBFAMILY ORTHOCLADIINAE

Cardiocladius platypus (Coquillett)

(Figs. 6–9)

Orthocladius platypus Coquillett 1902:93; type locality, Flagstaff, AZ.

Cardiocladius platypus (Coquillett); Sublette 1966:587, review; Oliver et al. 1990:21, catalog.

Because the original description by Coquillett (1902) and redescription by Sublette (1966) were based on an imperfect pinned holotype, the following data are provided to augment these descriptions.

MALE.—*Coloration*: Almost entirely blackish brown; humeral and pleural areas very slightly paler.

Head: Antenna with 13 flagellomeres. Antennal ratio 1.51–1.63 (3). Palpal proportions 86:156:187:250 (1) µm. Eyes reniform, with a slightly angular medial margin. Ocular ratio 0.56–0.60 (4). Clypeus rectangular, distinctly wider than high, about as wide as the antennal pedicel; clyp/ped ratio 0.96–1.20 (4); with 26–28 (4) setae. Temporal setae 8–12 (4), in a slightly staggered single row, reaching to 0.68 of the distance from the eye to midline of the head.

Thorax: Antepronotum almost parallel-sided, not produced at the dorsal apex (Fig. 6). Thoracic chaetotaxy: lateral antepronotals 7–10 (4); dorsocentrals 14–23 (5), anteriorly in a partial double row; acrostichials 13–21 (4); prealars 5–7 (5); supra-alars lacking; scutellars 30–32 (5), in a strewn pattern.

Wing: Membrane with microtrichia visible at 125X. Costa not produced beyond R_{4+5}, which ends distal to M_{3+4} at 0.22 of the distance between apex of M_{3+4} and M_{1+2}. R_{2+3} evanescent at apex. Venarum ratio 1.02–1.09 (3). Wing length 1.90–2.58 (3) mm. Squama with 31–52 (4) marginal setae, which are 3–4X at base, becoming 2X, then 1X near the alula. Wing vein setae: R 9–14 (4), R_1 1–4 (4), other veins without setae.

Legs: Foretibial spur length 62–74 µm (3); middle tibial spur lengths 52–68/24–40 µm (4); hind tibial spur lengths 80–102/26–40 µm (4). Pulvilli absent. Leg ratios: P I 0.68–0.69 (3); P II 0.43–0.49 (4); P III 0.52–0.55 (3). P III comb setae 9–14 (4). P III sensilla chaetica 3–6 (2).

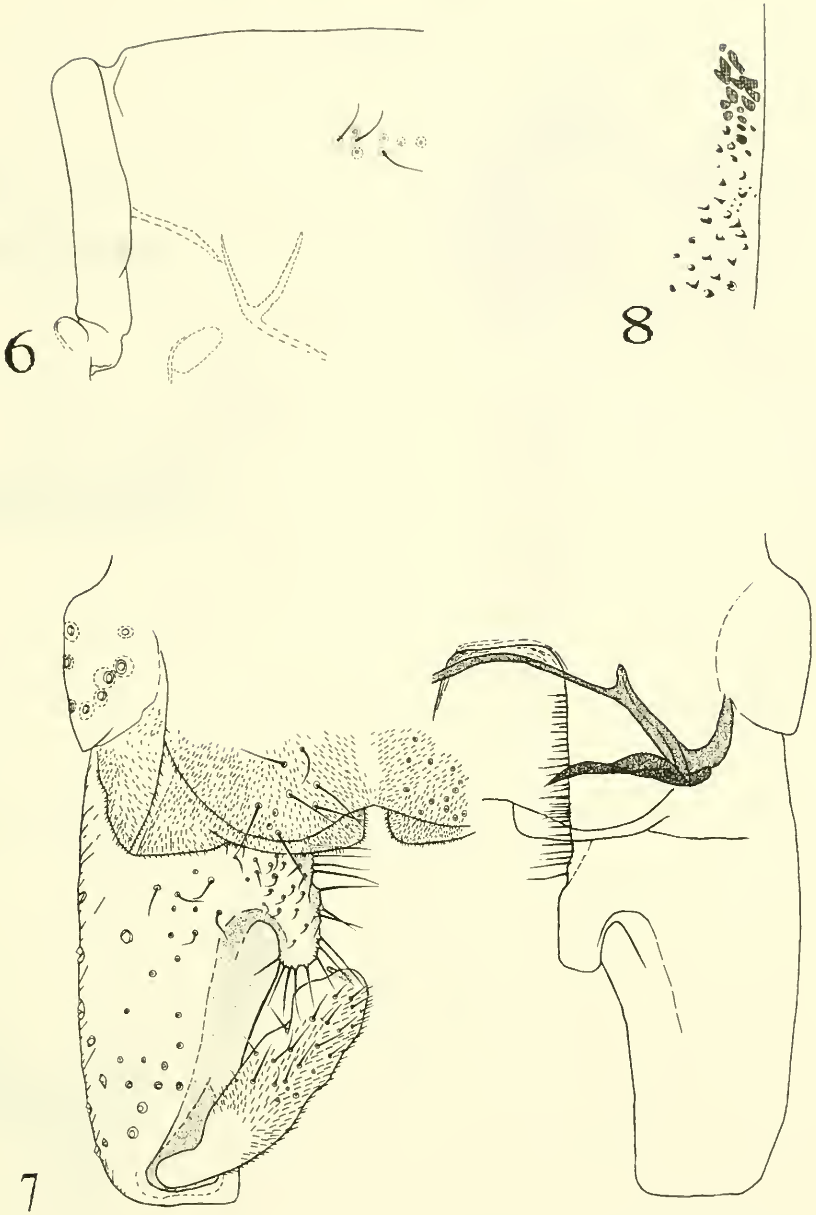
Genitalia (Fig. 7): Ninth tergum with 18 (2) setae. Gc/Gs ratio 1.80–1.81 (2).

PUPA (MALE).—Cephalothorax pale brown becoming dark brown posteriorly with a blackish spot over the base of each wing sheath. Abdomen yellowish brown becoming darker over the bases of the posterior tergal spine clusters; abdomen length 2.46–2.89 mm (3).

Cephalothorax: Setae absent on the frontal apotome, similar to that illustrated by Coffmann et al. (1986: Fig. 9.9A). Thoracic horn lacking. Median suture with strong tubercles on about middle 1/3 on either side; posteriorly the cephalothorax becomes rugose, then at extreme posterior end of the suture, fine, dark tubercles occur (Fig. 8). Precorneal setal cluster with 1 long (139 µm), 1 smaller (77 µm), and 1 very fine seta (62 µm). Dorsocentrals: Dc_1 coarse; Dc_2 smaller than, above, and slightly behind Dc_1; Dc_3 almost in a line with Dc_1 and about the same size; Dc_4 almost directly above Dc_3 and about the same size as Dc_2. Wing sheaths without baeatiform papillae or nasiform tubercles.

Abdomen: Shagreen pattern and chaetotaxy (Fig. 9); tergum I with an anterior and posterior band of spines; terga II–VIII with bands of spinulae and spines similar to that illustrated for tergum V, but virtually devoid of shagreen between median spinulae band and posterior band of spines; anterior to the median band on T II–VIII, each tergum is covered with weak shagreen. Anal macrosetae with the anterior 1 well separated from the posterior 2 and either simple and spinelike or with weak apical or subapical bifurcations (Fig. 9); length 146 µm; length of longer posterior macroseta 149 µm; ALR 0.73–1.15; sternum VIII (Fig. 9).

DIAGNOSIS AND DISCUSSION.—The dark coloration and features of the male genitalia (Fig. 7) differentiate *C. platypus* from other Nearctic species of *Cardiocladius*. *Cardiocladius obscurus* (Johannsen) has similar coloration and genitalia; however, the basidorsal gonocoxite lobe of that species (Sublette 1967; Fig. 7) is more rounded, costa slightly extended, and scutellum pale. The pupa of *Cardiocladius obscurus* has been illustrated by Johannsen (1937) and Coffman et al. (1986: Fig. 9.9A, B) as *C.* cf. *obscuripes* (Johannsen) (sic! = *obscurus*). It differs from *C. platypus*, described herein, in 2 noticeable features: the apical spines on terga I–VIII are longer and more numerous, and shagreen is virtually lacking on terga II–VII between median and posterior bands of denticles. Further, the L-setae of T VIII are heavier than in the species illustrated by Coffmann et al. (1986).

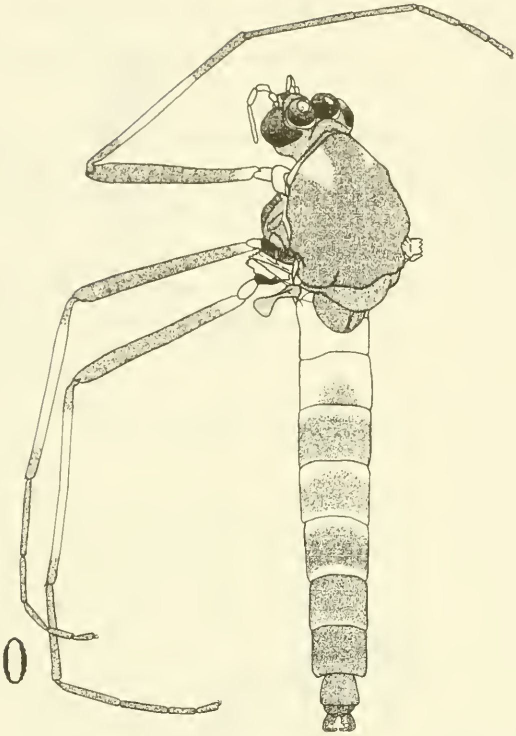


Figs. 6–8. *Cardiocladius platypus.* Male: 6, antepronotum, lateral view; 7, genitalia. Pupa: 8, cephalothoracic tubercles adjacent to median suture.

Pupae of the Palearctic species *C. fuscus* Kieffer and *C. capucinus* (Zetterstedt) differ among the features described and illustrated by Langton (1991).

ECOLOGY.—*Cardiocladius platypus* is an obligate, stenothermal rheophile that occurs throughout much of the upper Arkansas River in Colorado, with adults taken from 1497 to 3042 m elevation (Ruse et al. unpublished data). It has been taken in northern New Mexico (Sublette and Sublette 1979; unpublished records) in the Canadian, Rio Grande, and San Juan drainages. It occurs at stations with substrata ranging from rubble-gravel to gravel-sand.

DISTRIBUTION.—California to Colorado and New Mexico; Quebec (Oliver et al. 1990).



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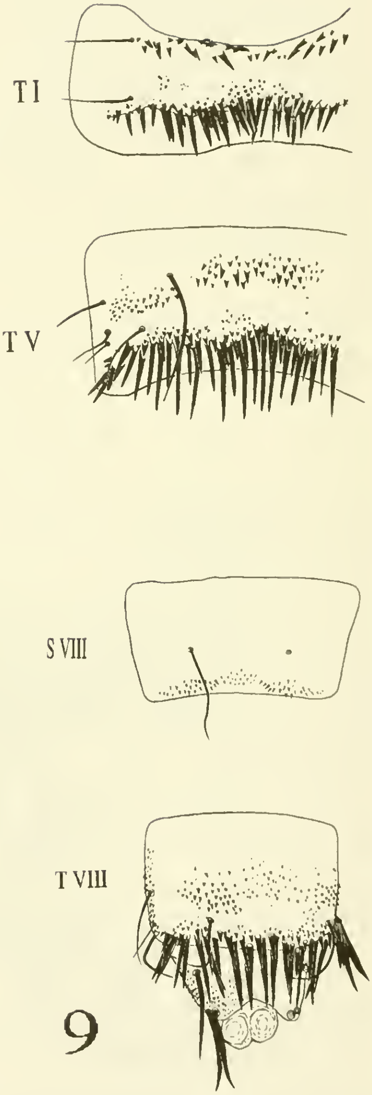

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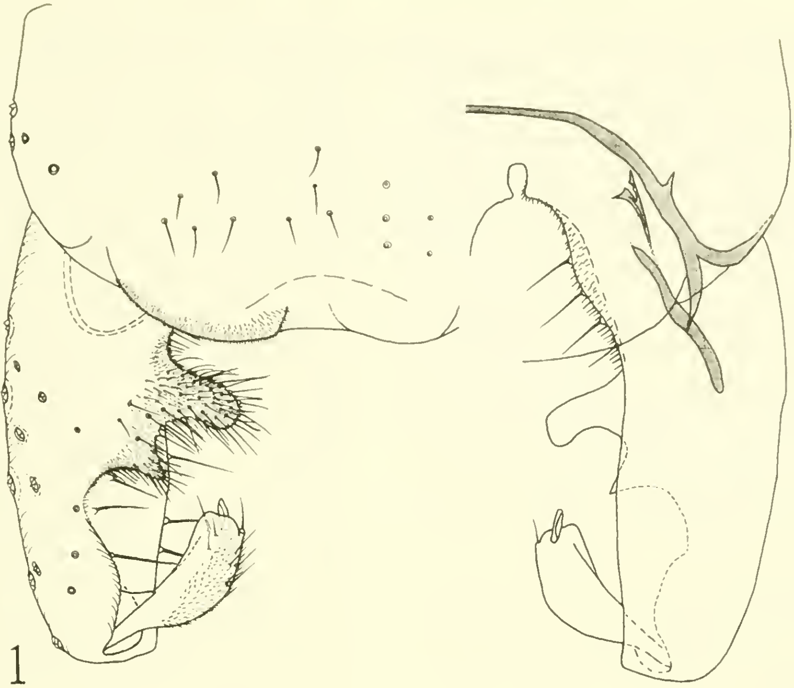
Figs. 9–10. *Cardiocladius platypus.* Pupa: 9, abdominal shagreen and chaetotaxy, terga I, V, VIII, anal lobe, and sternum VIII. *Cricotopus (Cricotopus) annulator.* Male: 10, coloration, semidiagrammatic.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♀, river mi 0.0, 947 m elev; 1 ♂, river mi 72.0, 796 m elev; 1 ♂, river mi 108.0, 699 m elev; 1 ♂, 1 Pex, river mi 151.2, 556 m elev; 1 ♂, river mi 153.0, 549 m elev; 1 ♂, river mi 157.0, 555 m elev; 1 ♂, river mi 202.0, 457 m elev; 1 ♀ Pex, river mi 205.7, 451 m elev. Additional specimens examined from California, Colorado, and New Mexico.

Cricotopus (Cricotopus) *annulator* Goetghebuer

(Figs. 10–12)

Cricotopus annulator Goetghebuer 1927:52; type locality, Belgium.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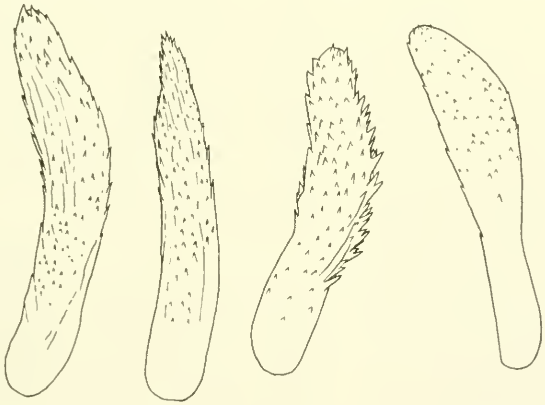
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Figs. 11–12. *Cricotopus* (*Cricotopus*) *annulator*. Male: 11, genitalia. Pupa: 12, thoracic horn variation.

Cricotopus irwini Sublette and Sublette 1971:97; type locality, California; male.

Cricotopus (*Cricotopus*) *irwini* Sublette & Sublette 1979:70, distribution, subgeneric position.

Cricotopus (*Cricotopus*) *annulator* Goetghebuer; Hirvenoja 1973:202, adults, immatures, distribution, synonymy; Laville 1979:160 and Rossaro 1987:333, ecology; LeSage and Harrison 1980a:73, adults, distribution, synonymy; 1980b:376, ecology; 1980c:2, biology of parasites; Simpson et al. 1983:4, adults, immatures, in key (after Hirvenoja 1973); Hudson et al. 1990:9, in list; Oliver et al. 1990:23; in catalog, synonymy; Langton 1991:219, pupa.

Cricotopus olivetus Boesel 1983:88; type locality, Ohio; male. *New synonym.*

The adult male and pupa differ slightly in some features from the description of Hirvenoja (1973). They are redescribed here to assist future comparisons.

MALE.—*Coloration* (Fig. 10): Head, fused thoracic vittae, preepisternum, and postnotum blackish brown; antepronotum and scutellum brown but usually paler than postnotum; humeral and pleural areas yellowish; legs dark with paler fasciae; abdomen fasciate, with dark brown bands interspersed with yellowish bands; genitalia yellowish at apex, somewhat infuscate basally.

Head: Antenna with 13 flagellomeres. Antennal ratio 1.11–1.30 (4). Palpal proportions 55–70 (3):94–101 (3):117–133 (3):195–203 µm (3). Eyes with dorsal extension short and wedge-shaped. Ocular ratio 0.44–0.48 (3). Clypeus at base 0.86 of width of antennal pedicel; with 11–12 (4) setae. Temporal setae 7–10 (4), in a single row, reaching to near the midline of the head.

Thoracic chaetotaxy: Lateral antepronotals 5–8 (3); dorsocentrals 14–21 (7), in a partial double row; acrostichials 16–22 (7), mostly in 2 rows; prealars 5 (3); supra-alars lacking; scutellars 7–8 (3).

Wing: Membrane with microtrichia visible at 300X. Costa extended 54–60 µm (3) beyond R_{4+5}, which ends distal to M_{3+4} at 0.16 of the distance between apex of M_{3+4} and M_{1+2}. R_{2+3} ends at 0.42–0.51 (3) of the distance between apex of R_1 and R_{4+5}. Venarum ratio 1.09–1.14 (3). Wing length 1.80–1.97 mm (3). Squama with 8–9 (3) marginal setae. Wing vein setae R 6–9 (3); other veins without setae.

Legs: Foretibial spur length 44 µm (3). Middle tibial spur lengths 22–24/18–20 µm (3); hind tibial spur lengths 46–52/16–22 µm (3). Apical tarsomere, claws, empodium, and hyaline lamellae; pulvilli absent. Leg ratios: P I 0.59–0.65 (7); P II 0.47–0.50 (3); P III 0.56–0.59 (3). P III sensilla chaetica 6–7 (3).

Abdomen: Abdominal tergal setae: III, medians 5 (2), laterals 12–13 (2); IV, medians 5–7 (3), laterals 13–15 (2).

Genitalia (Fig. 11): Ninth tergum with 6–14 (3) setae. Gc/Gs ratio 2.48–2.69 (3).

PUPA.—Exuviae pale brown on posterior part of cephalothorax and darker brown on terga II–VI. Abdomen length 2.20–3.04 mm. *Cephalothorax*: Frontal setae absent on the frontal apotome. Thoracic horn variable in shape (Fig. 12), length 120–161 µm. Median suture with weak rugosity anteriorly on either side. Precorneal setae are of about equal length but with 1 slightly heavier. Dorsocentrals are small, almost in a straight line. Wing sheaths are without bacatiform papillae or nasiform tubercles.

Abdomen: Shagreen pattern and chaetotaxy similar to that figured in Hirvenoja (1973: Fig. 122-12). Tergum II hooks 43–65, in 2 rows; T II with a posterior row of fine shagreen just in front of hook row and in some specimens also a median band of very weak shagreen. Pedes spurii B (PSB) present on T II and T III, the latter being somewhat smaller and less projecting. Tergum VI with an oval to almost round median shagreen patch of which the L/W is 0.43–0.67. Anal macrosetae length 118–148 µm; anal lobe length 195–234 µm; ALR 0.61–0.63.

DIAGNOSIS AND DISCUSSION.—Abdominal and leg color patterns and genitalia of Nearctic specimens are so similar to the Palearctic species *C. (Cricotopus) annulator* that various authors have considered the 2 populations to be conspecific. Excellent reared material from Grand Canyon National Park and elsewhere clearly demonstrates some slight differences in the pupa from that described by Hirvenoja (1973) and Langton (1991). Most notable is the posterior shagreen band on T II as well as the presence of PSB on both T II and T III. The PSB on T III is, however, smaller than that on T II and, on some specimens, difficult to discern. A reexamination of the adults shows a slight difference in color bands of the foretibia as well as a genitalic difference in the basidorsal gonocoxite lobe, which is usually downturned at the apex.

ECOLOGY.—*Cricotopus annulator* inhabits flowing water systems ranging from spring runs to large rivers on a variety of substrata and under wide-ranging environmental conditions. Larvae usually concentrate in areas of moderate current with continuous adult emergence, but with spring and fall emergences accounting for about 90% of emergences at temperatures of 15–16°C. Adult males swarm at stream banks at less than 1 m height above clumps of grass (LeSage and Harrison 1980b). In Italy the species has been taken from *Typha latifolia* L. along the margin of a stream (Rossaro 1987). In England it was associated with *Sparganium* sp. and fine sediments in the River Pang (Ruse 1992), and *Myriophyllum spicatum* L. in a small stream, the River Tud (Tokeshi and Townsend 1987). Cobo and Gonzáles (1991) found it in relatively low numbers at 2 of 5 organically polluted sites on the River Sar in Spain. Schmid (1993) reported it in Austria in relatively low numbers among surface and gravel interstitial-dwelling larvae in a coldwater, gravel-bottomed stream. Similarly, Kownacki (1982) reported it to be relatively uncommon in a small pastureland stream in Poland. Anderwald et al. (1991) reported it from the Danube, a large river. In Germany, Kownacki and Margreiter-Kownacka (1993) found *C. annulator* in the soft sediments of the Alz River below a lake outflow as well as the firmer sediments of the lower stretches of the stream. Laville and Lavandier (1977) found this species at higher elevations in colder water over boulder-gravel substrata which had some moss and detritus in the French Pyrenees. In the Ossau Valley this species occurred at 500–2000 m elevation at maximum temperatures of 12–15°C (Laville and Vinçon 1991). In Lebanon, Moubayed and Laville (1983) reported *C. annulator* from the Beirut River at 700 m elevation, in slow to very slow summertime water flows, at a station with mosses in the current and macrophytes on the stream margins. Sublette and Sublette (1979) reported this species as being widely distributed in northern New Mexico streams, including the San Juan River, an upper tributary of the Colorado River. In the upper Arkansas River of Colorado it was taken at 1497–2743 m elevation on substrata that varied from boulder-cobble to gravel-sand (Ruse et al. unpublished data).

DISTRIBUTION.—This Holarctic species is widely distributed in the Nearctic region from California to Labrador.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 256 ♂♂ (some reared), 16 ♀♀ (some reared), 18 PP, throughout the river corridor from river mi 0.0, 947 m elev, to river mi 269.5, 356 m elev.

Cricotopus (Cricotopus) blinni

Sublette, new species

(Figs. 13–20, 54, 55)

HOLOTYPE MALE.—Grand Canyon National Park, Coconino Co., AZ, Colorado River mile 144.0, 570 m elev, 25-X-90, J.S., slide no. P0014 (CAS).

Coloration (Fig. 13): Head, thoracic vittae, scutellum, preepisternum, and postnotum blackish brown; antepronotum, humeral and pleural areas yellowish; legs dark with only trochanters and extreme base of all femora paler; abdomen fasciate, with T IV entirely yellowish and the genitalia dark.

Head (Fig. 54a): Antenna with 12 flagellomeres. Antennal ratio 1.02 (0.96–1.16; 11). Palpal proportions 47:86:117:148 µm (42–55:86–90: 109–117:148–187 µm; 6). Eyes with dorsal extension short and wedge-shaped; ocular ratio 0.43 (0.41–0.50; 6). Clypeus trapezoidal, about as wide at base as width of antennal pedicel; with 16 (8–16; 6) setae. Temporal setae 6 (6–8; 6), of which 2 (2–3; 6) are inner verticals near midline of the head, clearly separated from the 4 (4–6; 6) postoculars.

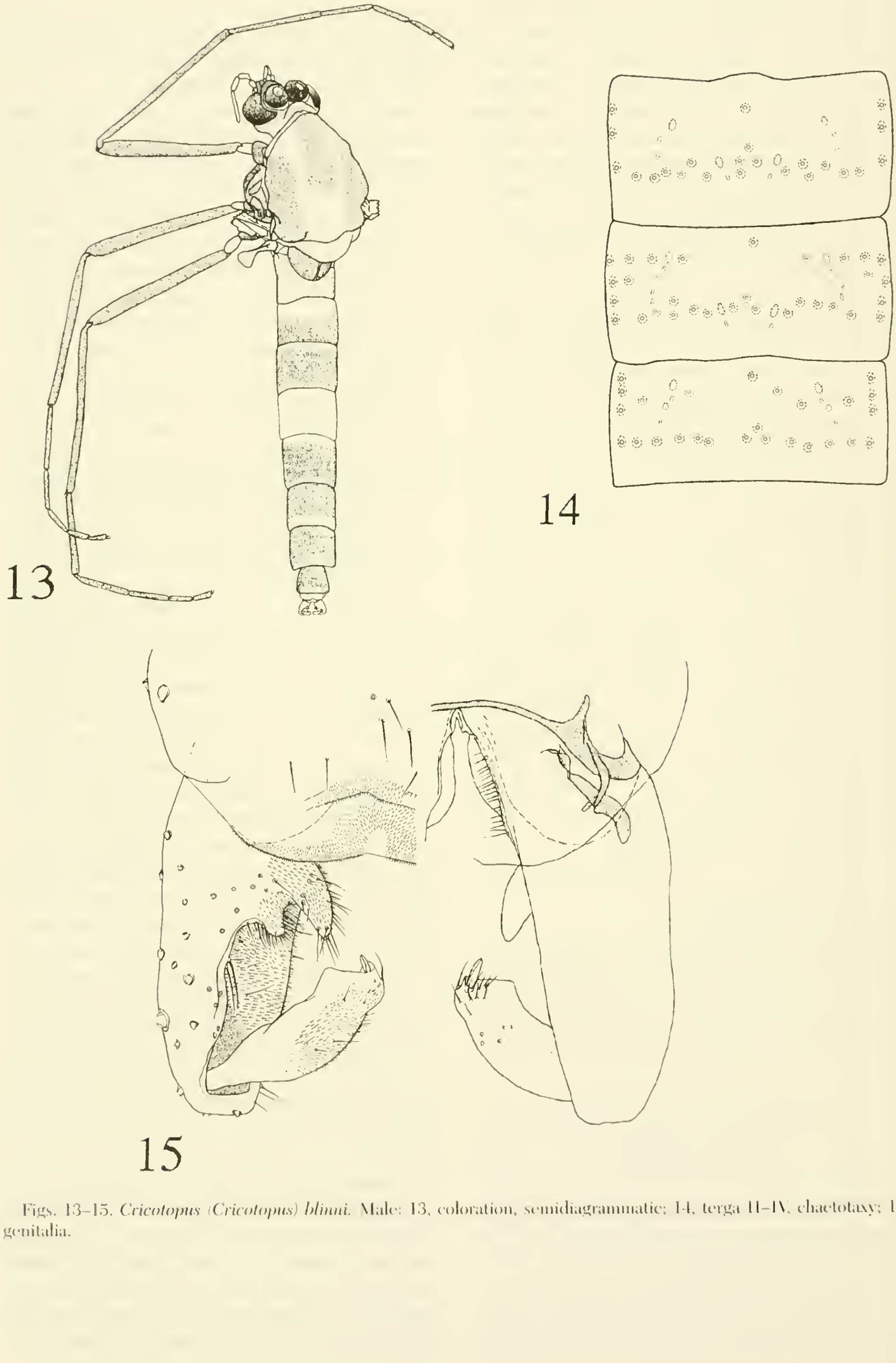
Thorax (Fig. 54a): Antepronotum almost parallel-sided near the dorsal apex. Thoracic chaetotaxy: lateral antepronotals 5 (5–9; 6); dorsocentrals 17 (11–25; 6), in a partial double row; acrostichials 18 (15–20; 6), mostly in 2 rows; prealars 4 (3–5; 6); supra-alars lacking; scutellars 17 (13–20; 6), in a strewn pattern.

Wing: Membrane with microtrichia visible at 300X. Costa extended 52 (13–56; 6) µm beyond R_{4+5}, which ends distal to M_{3+4} at 0.22 of the distance between apex of M_{3+4} and M_{1+2}. R_{2+3} ends at 0.48 (0.51–0.59; 6) of the distance between apex of R_1 and R_{4+5}. Venarum ratio 1.14 (1.11–1.21; 6). Wing length 1.94 (1.54–1.97; 6) mm. Squama with 5 (2–5; 6) marginal setae. Wing vein setae: R 4 (2–4; 5), R_{4+5} 0 (0–1; 6); other veins without setae.

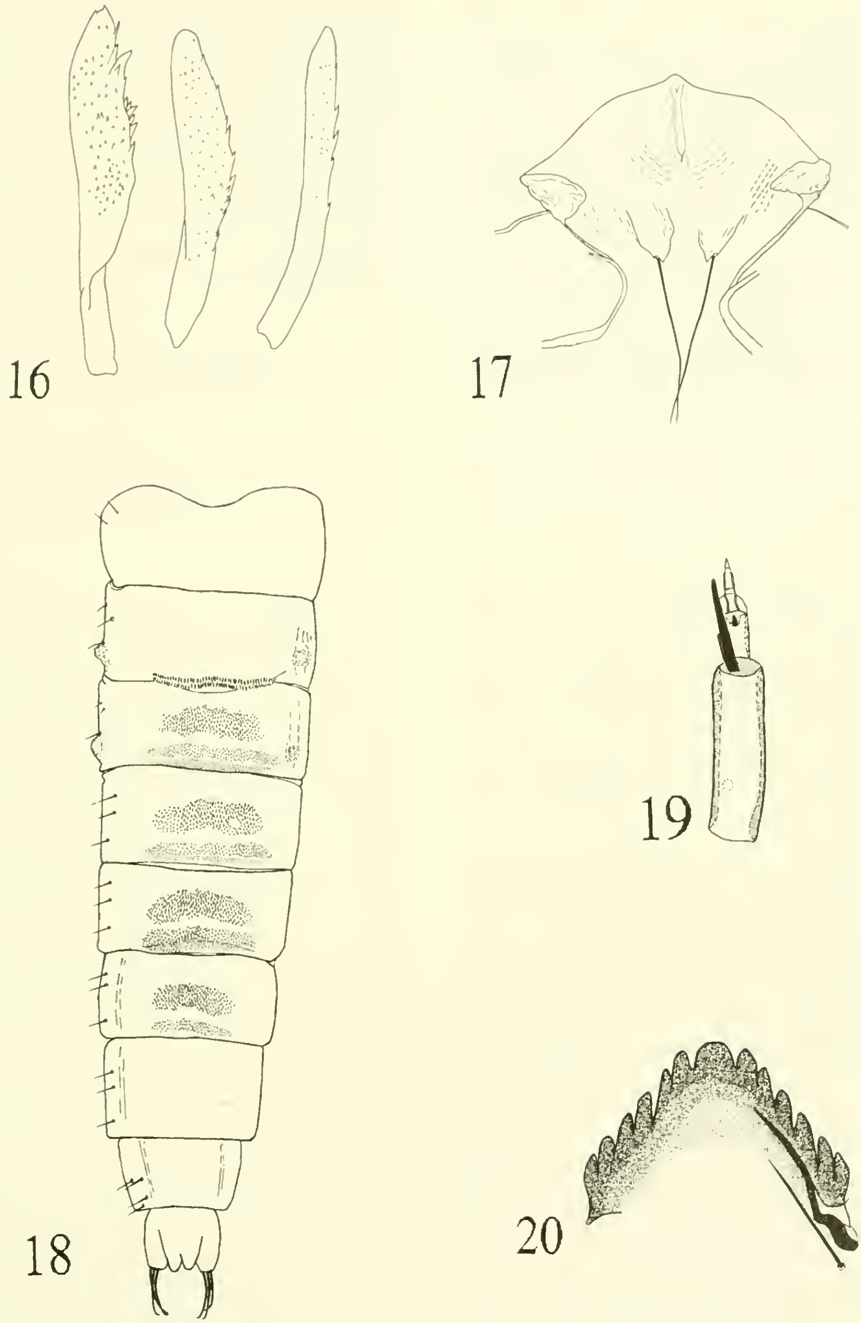
Legs: Foretibial spur length 42 (36–44; 5) µm; middle tibial spur lengths 22/20 (24–26/ 22–26; 5) µm; hind tibial spur lengths 56/24 (46–60/20–28; 5) µm. Apex of tarsomere 5, claws, hyaline lamellae, empodium and ungitractor (Fig. 54e), pulvilli vestigial. Leg ratios: P I 0.59 (0.58–0.62; 5); P II 0.44 (0.45–0.48; 5); P III 0.57 (0.53–0.58; 5). P III comb setae 14 (12–17; 5). P III sensilla chaetica 6 (5–9; 5).

Abdomen: Tergal setal pattern T II–T IV (Fig. 14); setae: III, medians 4 (4–7; 5), laterals 13 (9–13; 5); IV, medians 4 (4–6; 5), laterals 11 (7–19; 5).

Genitalia (Figs. 15, 54c): Ninth tergum with 13 (10–14; 5) setae. Gc/Gs ratio 2.0 (2.03–2.24; 5). Slide mounts of this (and other) species show much variation in the gonostylus, depending on the orientation; Figures 54f–h show the appearance of the gonostylus in various rotational positions. Apex of basidorsal gonocoxite lobe without dorsal microtrichia (Fig. 54c).



Figs. 13–15. *Cricotopus (Cricotopus) blinni.* Male: 13, coloration, semidiagrammatic; 14, terga II–IV, chaetotaxy; 15, genitalia.



Figs. 16–20. *Cricotopus (Cricotopus) blinni*. Pupa: 16, thoracic horn variation; 17, frontal apotome; 18, abdominal shagreen and chaetotaxy. Larva: 19, antenna; 20, mentum.

PUPA.—Abdomen length 2.04–2.65; 2.36 mm (6). *Cephalothorax*: Cephalothorax pale brown. Frontal setae present on the frontal apotome (Fig. 17); frontal setal length 86–152 µm (2). Thoracic horn variation (Fig. 16), length 170–226; 189 µm (6). Median suture of cephalothorax with strong rugosity on either side; lateral surface of cephalothorax with weak, scalelike tubercles. Precorneal setae subequal in length with 1 very slightly weaker than the other 2. Dorsocentrals small, almost in a line. Wing sheaths without bacatiform papillae or nasiform tubercles.

Abdomen: Abdominal terga I–VI pale brown. Shagreen pattern and chaetotaxy (Fig. 18); details of shagreen on tergum III (Fig. 54b). Tergum II hooks 59–84; 66 (7), in 2 rows (Fig. 54d). Pedes spurii B present on terga II and III. Anal lobe length 198–201 μm (4); anal macrosetae length 130–155; 145 μm (4). ALR 0.73–0.80; 0.77 (4).

LARVA.—Ventral head length 164–187 μm (3). Head entirely pale except for darkened occipital ring, tips of the mandible, and mentum.

Antenna (Fig. 19): Blade shorter than flagellum; lauterborn organs large, extending to apex of 3rd segment; ring organ at 0.23 from the base.

Epipharyngeal region (Fig. 55b): S I apically bifurcate; pecten epipharyngis of 3 unequal blades which are apparently fused (Fig. 55b); chaetae 5; spinulae about 3; chaetulae laterales 7, variable in size and shape; chaetulae basales 2, weakly dissected apically. Ungula V-shaped with the basal sclerite quadrangular. Premandible with 1 apical tooth and a slight subapical shelf; brush lacking.

Maxilla (Fig. 55e): Lacinial chaetulae 5; antaxial seta shorter than lacinial chaetulae; paraxial seta shorter than antaxial seta; palpus with 13 sensillar structures (Fig. 55d).

Mandible (Fig. 55a): Apical tooth shorter than combined width of the 3 inner teeth; seta subdentalis apically pointed; seta interna (not shown) with 3 main branches which are simple; outer margin moderately crenulate; mola smooth.

Mentum (Fig. 20): Median tooth <2X width of 1st laterals; 2nd lateral slightly shorter than 1st and 3rd. Anterior parapods pectinate (Fig. 55c), with claws progressively diminishing in size posteroventrally.

DIAGNOSIS AND DISCUSSION.—The genitalia and chaetotaxy resemble those of the *festivellus*-group (Hirvenoja 1973), but members of that group have P II sensilla chaetica which are lacking in this species; also the abdominal color pattern of this species is distinctively different. It also closely resembles *C.* (*Cricotopus*) *herrmanni* Sublette, new species, in genitalic features and abdominal chaetotaxy, but that species has a significantly lower antennal ratio and a strikingly different color pattern. The larva is also similar to members of the *festivellus*-group, but the central tooth of the mentum is much narrower than in known members of that group. The pupa is similar to the Palearctic species *C. albiforceps* Kieffer (Hirvenoja 1973: Fig. 140), but that species has pedes spurii B only on tergum II, while this species has both PSB II and III. Also, the thoracic horn appears to be less spinose. The pupa is very similar to that of *C.* (*Cricotopus*) *herrmanni* Sublette; however, the length of the thoracic horn is usually less than that of *C. herrmanni*, and the anal macrosetae are shorter than 125 μm.

ECOLOGY.—This species is widely distributed in the cold, swift Colorado River corridor, with specimens collected from Lees Ferry to mile 166.5. Adults were collected from July to February.

DISTRIBUTION.—California to Colorado and New Mexico.

PARATYPES.—AZ: 2 ♂♂, collected with the holotype (NAU). Mohave Co., 1 ♂, Colorado R, Bullhead City, 5-IX-73, M.S. Mulla (UCR). Coconino Co., 1 L, Colorado R, Grand Canyon National Park, river mi 0.5, 950 m elev; 2 ♂♂, river mi 133.0, 597 m elev; 1 ♀, river mi 133.5, 600 m elev; 1 ♂, river mi 144.0, 572 m elev; 1 ♂, river mi 166.5, 532 m elev.

CA: Riverside Co., 3 ♂♂, Laflin Ranch, between Thermal and Mecca, 15-V-70, lt. tr. (UCR); San Bernardino Co., 7 ♂♂, Spring Valley L, 11-IX-73, M.S. Mulla (UCR, JES).

CO: Lake Co., 1 ♂, 4 ♀♀, E fork of Arkansas R, 3042 m elev, 20–21-IX-84, S.J. Herrmann. Pueblo Co., 69 ♂♂, Arkansas R, Pueblo Blvd Br, 1431 m elev, 31-X–1-XI-84, 4-XI-84, S.J. Herrmann; 9 ♂♂, 22-VIII-83, P. Sanchez; 70 ♂♂, Stilling Basin Br, below Pueblo Res, 1444 m elev, 10-VI-85, 15-VIII-85, 18-IX-85, 17-VII-87, S.J. Herrmann; 6 ♂♂, Hobson Ranch, 1504 m elev, 19-IX-85, 17-VII-87, S.J. Herrmann. Fremont Co., 10 ♂♂, Portland Br, 1535 m elev, 21-III-85, 19-IX-85 (SJH, JES, UC, KU, ANSP, CAS, AEI, CNC, USNM, INHS, UMN, BYU).

NM: Santa Fe Co., 22 ♂♂, Rio Grande, Otowai Br, near San Ildefonso Pueblo, 8-IX-74, 5-X-74, 16-VII-76, malaise trap, sweep net, M. Beard (JES). Socorro Co., 1 ♂, Rio Grande, nr San Marcial, 11-VII-76, sweep net, M. Beard. Doña Ana Co., 6 ♂♂, Rio Grande, at Texas state line, 15-XI-74, M. Beard. Catron Co., 8 ♂♂, 1 ♀, San Francisco R, south of Pleasanton, nr Frisco Hot Spgs, 10-VII-74, 17-IX-74, malaise trap, 18–24-XI-74 (reared), M. Beard (JES). Quay Co., 4 ♂♂, Canadian R, at mouth of Revelto Cr, 1-X-74, M. Beard. Colfax Co., 3 ♂♂, Canadian R, Hwy 54, at Taylor Spgs, 3-X-74, sweep net, M. Beard. San Juan Co., 1 ♂, San Juan R, 1 mi W San Juan Co. Hospital, 18-VII-76, M. Beard, J.E. Sublette (JES).

This species is dedicated to Dr. Dean W. Blinn, limnologist at Northern Arizona University, Flagstaff, for his assistance in bringing this project to fruition.

Cricotopus (Cricotopus) globistylus Roback

(Figs. 21–32, 56)

Cricotopus globistylus Roback 1957:10, male and female, type locality, Heber-Midway bridge, Wasatch Co., Utah; Sublette and Sublette 1979:69, in list; Oliver et al. 1990:25, catalog.

The male has been very briefly described and inadequately illustrated (Roback 1957). The following is a more complete description of the male together with descriptions of the pupa and larva.

MALE.—*Coloration* (Fig. 21): Head, thoracic vittae, preepisternum, and postnotum blackish brown; antepronotum and scutellum paler than postnotum; humeral and pleural areas yellowish; legs dark; abdomen fasciate, with dark brown bands interspersed with yellowish bands; genitalia dark.

Head: Antenna with 13 flagellomeres. Antennal ratio 0.63–1.17; 0.82 (17). Palpal proportions 39–78:86–140:86–117:125–164 μm. Eyes with dorsal extension short, wedge-shaped. Ocular ratio 0.44–0.53 (3). Clypeus quadrangular, slightly wider at base than width of antennal pedicel; with 6–19 (15) setae. Temporal setae 10–13 (6), in a slightly staggered single row, reaching near midline of head.

Thorax: Antepronotum moderately produced at dorsal apex (Figs. 22, 56a). Thoracic chaetotaxy: lateral antepronotals 8–14; 11 (5); dorsocentrals rather coarse, 17–25 (6), in a partial double row (Fig. 56a); acrostichials 10–18 (6), mostly in 2 rows; prealars 3–7 (6); supra-alars absent; scutellars 21–38 (6), in a strewn pattern.

Wing: Membrane with microtrichia visible at 300X. Costa extended 28–50 μm beyond R_{4+5}, which ends distal to M_{3+4} at 0.39 of the distance between apex of M_{3+4} and M_{1+2}. R_{2+3} ends at 0.34–0.45 (6) of the distance between apex of R_1 and R_{4+5}. Venarum ratio 1.0–1.05 (6). Wing length 1.47–2.23 (6) mm. Squama with 4–10 (6) marginal setae. Wing vein setae: R 6–14 (6); other veins without setae.

Legs: Foretibial spur length 48–71 (6) μm; middle tibial spur lengths 31–37/20–30 (6) μm; hind tibial spur lengths 56–74/22–36 (6) μm. Pulvilli absent. Leg ratios: P I 0.53–0.57 (6); P II 0.37–0.44 (6); P III 0.46–0.53 (6). P III comb setae 7–13 (6). P III sensilla chaetica 5–10 (6).

Abdomen: Abdominal tergal setae (Fig. 23): T III, medians 5–13 (6), laterals 11–22 (6); T IV, medians 8–13 (6), laterals 12–27 (6).

Genitalia (Fig. 24): Ninth tergum with 5–16 (6) setae. Gc/Gs ratio 2.31–2.48 (6).

PUPA.—Exuviae pale brown except for darker brown shagreen patches. Abdomen length 2.65–3.08 mm (5).

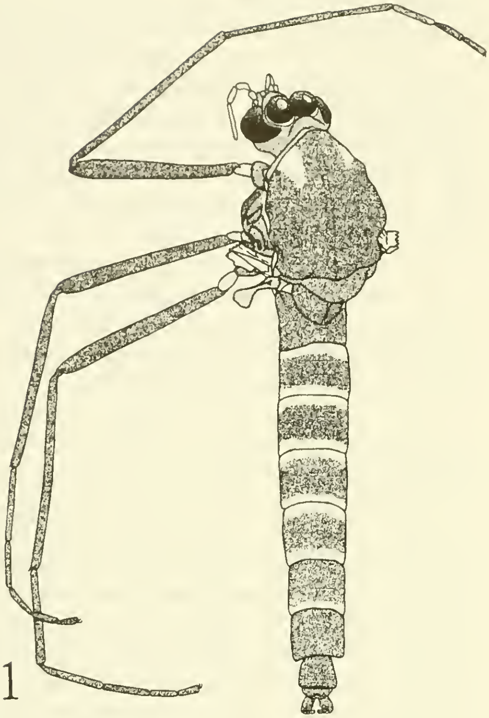
Cephalothorax: Frontal setae present but frequently lost. Thoracic horn (Fig. 25), length 88–108 μm (5). Median suture with weak rugosity on either side. Precorneal setae with 1 long and 2 slightly smaller setae. Dorsal antepronotal seta much longer than ventral. Dorsocentrals small, almost in a line. Wing sheaths without bacatiform papillae or nasiform tubercles.

Abdomen: Shagreen pattern and chaetotaxy (Figs. 26, 56b–d). Tergum II hooks 57–72 (5), in 2 rows (Figs. 26, 56e,f); anterior to the hook row is a weak band of fine shagreen, which is occasionally absent. Pedes spurii B present on tergum II, broad and poorly defined. Pedes spurii A present on terga III–VI. Anal macrosetae length 125–127 (5) μm, heavy and only weakly curved at the tip, occasionally bifurcate; ALR 0.43–0.59 (5). Tergum VIII with 5 L-setae or occasionally with 4 only (as shown in Fig. 26).

LARVA.—Ventral head length 257 μm. Head pale brown with posterolateral margin dark, as are the occipital ring and tips of the mandible and mentum.

Antenna: With 5 segments (Fig. 27); length 99 μm; blade shorter than the flagellum, extending to level of 3rd segment; lauterborn organs moderately large but not reaching apex of 3rd segment; ring organ at 0.29 from base of 1st segment.

Epipharyngeal structures (Fig. 28): S I apically bifurcate; pecten epipharyngis of 3 unequal blades; chaetae 8; spinulae 5; chaetulae laterales 6; chaetulae basales 2, weakly fimbriate apically; ungula V-shaped with basal sclerite quadrangular. Premandible with 1 apical tooth; brush lacking.



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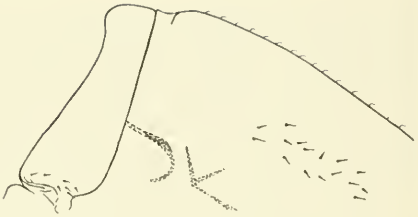

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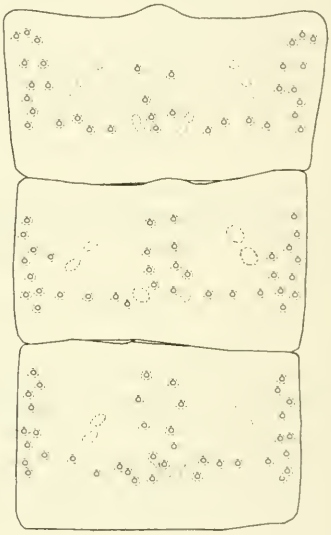

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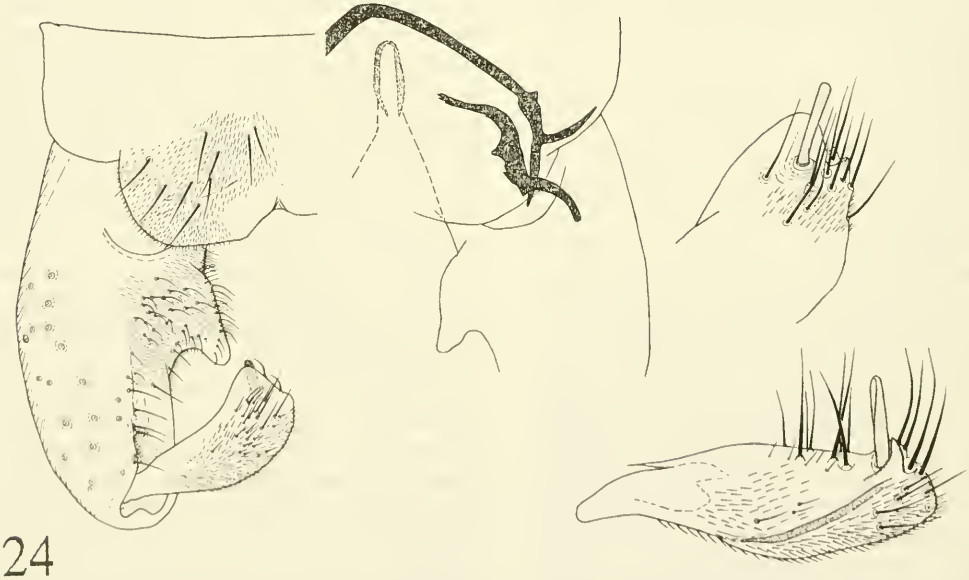

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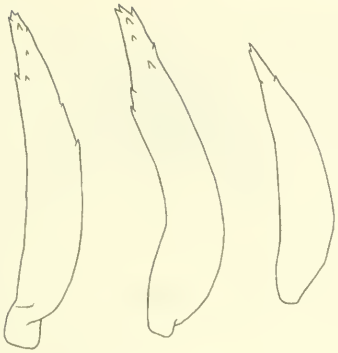
Figs. 21–24. *Cricotopus (Cricotopus) globistylus*. Male: 21, coloration, semidiagrammatic; 22, antepronotum, lateral view; 23, terga II–V chaetotaxy; 24, genitalia (left, dorsal; middle, internal skeleton; right, 2 views of gonostylar apex).



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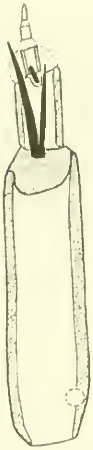

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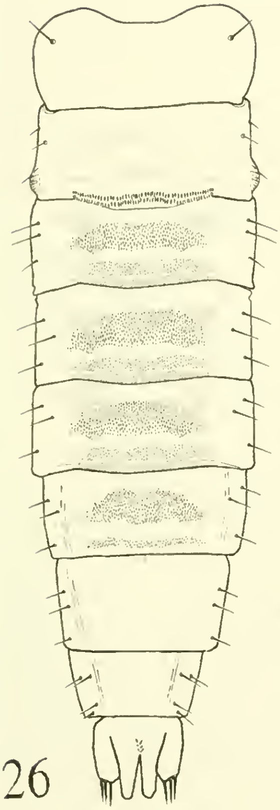

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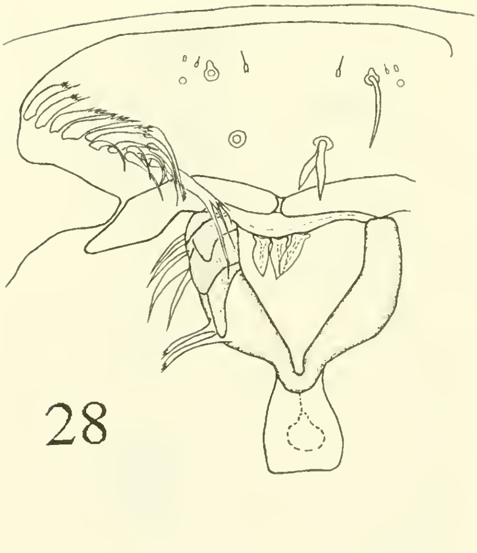

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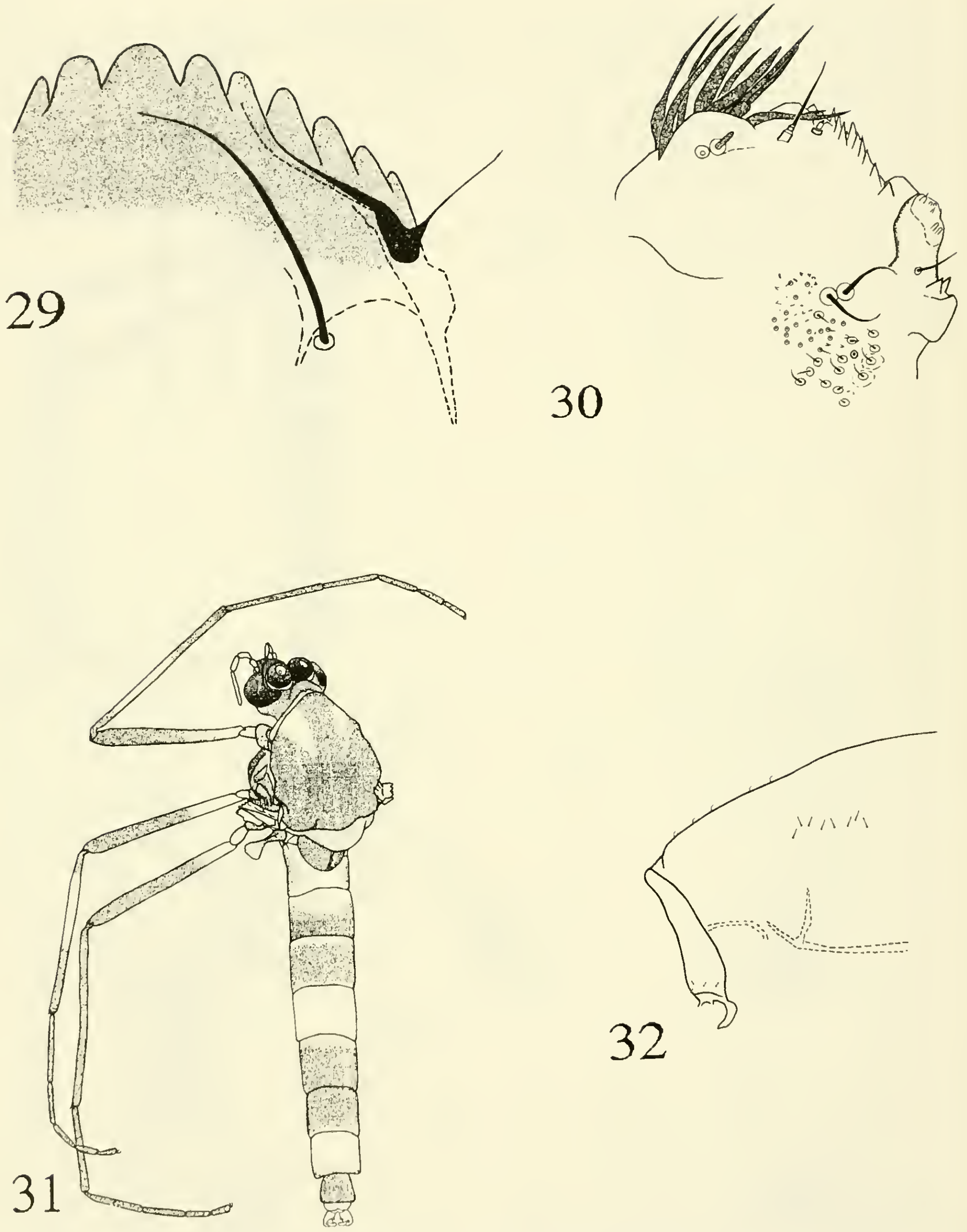
Figs. 25–28. *Cricotopus* (*Cricotopus*) *globistylus*. Pupa: 25, thoracic horn variation; 26, abdominal shagreen and chaetotaxy. Larva: 27, antenna; 28, epipharyngeal structures.

Mandible: Apical tooth shorter than combined width of 3 inner teeth; seta subdentalis apically notched; seta interna not discernible; outer margin strongly crenulate; mola smooth.

Mentum (Fig. 29): One median tooth which is <2X 1st laterals that are larger than remainder, which diminish in size laterally.

Maxilla (Fig. 30): Lacinial chaetae with 6 large anterior and about 4 smaller posterior blades; palpi slightly longer than wide.



Figs. 29–32. *Cricotopus (Cricotopus) globistylus*. Larva: 29, mentum; 30, maxilla. *Cricotopus (Cricotopus) herrmanni*. Male: 31, coloration, semidiagrammatic; 32, antepronotum, lateral view.

Body: With abdominal hair clusters of 1–4 setae up to 189 µm long; procercus dark brown, about as wide as high, with 1 long and 1 short setae on posterior face and 6 long terminal setae; each posterior parapod with about 13 yellowish brown claws.

DIAGNOSIS AND DISCUSSION.—The abdominal chaetotaxy, massive gonostylus, and fused basiventral and basidorsal lobes of the gonocoxite distinguish the male of this species from all other Holarctic *Cricotopus*. In Hirvenoja (1973) *C. globistylus* keys to the *fuscus*-group;

however, in that group the basidorsal and basiventral lobes are more or less separated and no species has such a massive gonostylus. The pupa, which lacks frontal setae, a scarcely discernible PSB on T II, a small, weakly spinose thoracic horn, shagreen patches on T III–VI well separated, and a weak L-seta on T VIII, does not fit any of Hirvenoja's groups. The larva, which has a central tooth of the mentum that is less than twice the width of the 1st laterals, also does not fit any of Hirvenoja's groups.

ECOLOGY.—This species occurs most often in cold streams with gravel bottoms. In Grand Canyon it is most common in the uppermost, clearwater reach above the Paria River confluence.

DISTRIBUTION.—Known from California north to Oregon and east to Montana and New Mexico.

MATERIAL EXAMINED: AZ: Coconino Co., Grand Canyon National Park, Colorado River, 74 ♂♂ (some reared), 8 ♀♀ (some reared), 27 Pex, river mi 0.0, 947 m elev, to river mi 109.0, 710 m elev. UT: Paratype ♂, Wasatch Co., Heber-Midway Br, 26-XI-54, Gerald D. Brooks (ANSP). Also, specimens, including reared material, from California, Oregon, Idaho, Montana, and New Mexico (CAS, USNM, JES).

Cricotopus (Cricotopus) herrmanni Sublette, new species

(Figs. 33–35, 57)

HOLOTYPE MALE.—Arkansas River, Fremont Co., CO, Canyon City, 9th street bridge, T85S, R70W, S33, 1618 m elev, 19-IX-85, S.J. Herrmann (CAS).

Coloration (Fig. 31): Head, thoracic vittae, preepisternum, scutellum, and postnotum blackish brown; antepronotum, humeral and pleural areas yellowish; legs dark with paler fasciae; abdomen fasciate, with dark brown bands interspersed with yellowish bands; genitalia yellowish at apex, somewhat infuscate basally.

Head: Antenna with 13 flagellomeres. Antennal ratio 0.58 (0.40–0.62; 12). Palpal proportions 47 (47–62; 6):86 (78–94; 6):109 (101–117; 6):[terminal palpomere on holotype shriveled] (156–211; 6) µm. Eyes with dorsal extension short and wedge-shaped. Ocular ratio 0.43 (0.40–0.46; 6). Clypeus quadrangular, slightly narrower at base than width of the antennal pedicel; with 8 (7–11; 6) setae. Temporal setae 9 (6–9; 6), of which 4 are inner verticals near the midline of the head widely separated from the remainder.

Thorax: Antepronotum almost parallel-sided in apical half (Fig. 32). Thoracic chaetotaxy: lateral antepronotals 6 (3–6; 6); dorsocentrals 18 (13–19; 6), in a partial double row, with the posterior setae distinctly coarser than the anterior; acrostichials 15 (14–21; 6), partially in 2 rows; prealars 4 (3–5; 6); supra-alars lacking; scutellars 15 (16–21; 6), irregularly biserial laterally becoming uniserial towards the middle, but with a median gap.

Wing: Membrane with microtrichia visible at 300X. Costa extended 60 (48–70; 6) µm beyond R_{4+5}, which ends distal to M_{3+4} at 0.26 of the distance between apex of M_{3+4} and M_{1+2}. R_{2+3} ends at 0.56 of the distance between apex of R_1 and R_{4+5}. Venarum ratio 1.24 (1.14–1.20; 6). Wing length 1.68 (1.52–1.90; 6) mm. Squama with 4 (3–5; 6) marginal setae. Wing vein setae: R 3 (3–5; 6), other veins without setae.

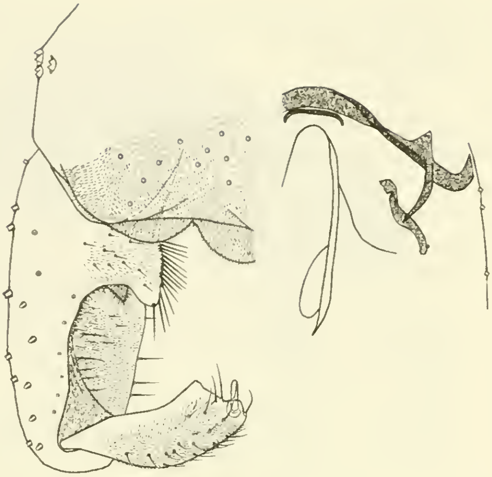
Legs: Foretibial spur length 44 (32–50; 6) µm; middle tibial spur lengths 26/24 (20–28/14–24; 5) µm; hind tibial spur lengths 58/26 (44–60/20–30; 6) µm. Pulvillus vestigial but hyaline lamella and empodium well developed. Leg ratios: PI 0.59 (0.58–0.64; 6); P II 0.47 (0.44–0.47; 6); P III 0.58 (0.51–0.59; 6). P III comb setae 13 (12–16; 6), with tips of the comb setae forming an arc. P III sensilla chaetica 7 (6–10; 7).

Abdomen: Abdominal tergal setae: T III, medians 6 (4–8; 6), laterals 10 (8–12; 6); T IV, medians 4 (4–7; 6), laterals 10 (5–13; 6); setal pattern similar to *C. blinni*, n. sp.

Genitalia (Figs. 33, 57a): Ninth tergum with 10 (11–22; 6) setae. Gc/Gs ratio 2.22 (2.04–2.40; 6). As in other species of *Cricotopus*, the gonostylus shows considerable variation in appearance due to position at the time of slide mounting; Figures 57b–d illustrate some of the variation observed at various angles due to slide-mounting differences.

PUPA.—*Exuviae*: Almost entirely pale brown; tergum VI still darker brown.

Cephalothorax: Frontal setae 60–70 µm (2). Thoracic horn (Fig. 34), length 214–275; 252 µm (7). Median suture with moderate rugosity on either side; lateral surface with weak, scale-like tubercles. Precorneal setae, 2 large, 1 slightly smaller. Dorsocentrals small, almost in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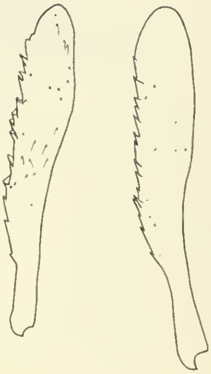
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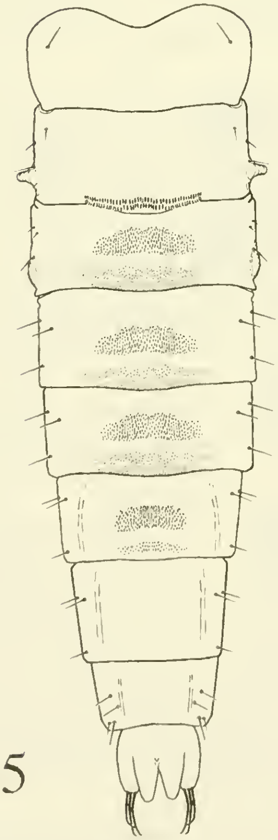
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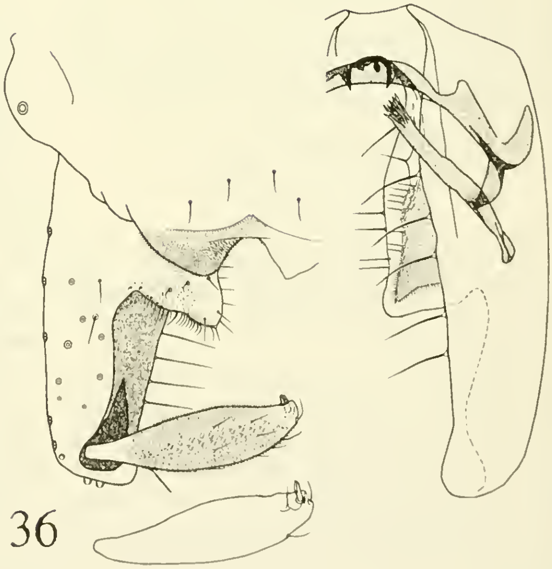
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Figs. 33–36. *Cricotopus (Cricotopus) herrmanni.* Male: 33, genitalia. Pupa: 34, thoracic horn variation; 35, abdominal shagreen and chaetotaxy. *Eukiefferiella ilkleyensis.* Male: 36, genitalia.

a straight row. Wing sheath without bacatiform papillae or nasiform tubercles.

Abdomen: Abdomen length 2.42–2.89 mm (5). Shagreen pattern and chaetotaxy (Fig. 35). Tergum II with 67–82; 71 (5) hooks in 2 very regular rows. Pedes spurii B present on terga II and III, with the PSB on II large and projecting and that on III smaller and rounded. Width of medial shagreen band on T III less than posterior. Medial shagreen of T VI L/W 0.31–0.37 (3). Anal lobe length 195–234; 214 µm (7). Anal macrosetae length 156–172; 162 µm (7). ALR 0.0.69–0.83; 0.76 (7).

DIAGNOSIS AND DISCUSSION.—The adult can be clearly differentiated from *C. blinni* by the distinctively different coloration (cf. Figs. 13, 31). The genitalia are very similar to those of *C. blinni* as well as members of the *cylindraceus*-group and *festivellus*-group (Hirvenoja 1973); however, these 2 groups differ in color. The pupa is very similar to that of *C. blinni*, but it has a slightly longer thoracic horn and longer anal macrosetae.

ECOLOGY.—This species has been collected most frequently from coldwater streams with gravel-sand substrata.

DISTRIBUTION.—California to Colorado and New Mexico.

PARATYPES AND MATERIAL EXAMINED.—AZ: Coconino Co., 1 ♂, Grand Canyon National Park, Colorado R, river mi 31.0, 876 m elev; 4 ♂♂, river mi 31.8, 876 m elev; 2 ♂♂, river mi 133.0, 597 m elev. Cochise Co., 1 ♂, Southwestern Research Station, 1646 m elev, V. Roth (UCR).

CA: 1 ♂, Davis, R.O. Schuster (UCD); 1 ♂, Hopeland, E.P. Van Duzee (CAS); 1 ♂, Oakland, E.S. Rosa (CAS); 1 ♂, Tule R, Springville, W.W. Wirth (USNM); 1 ♂, Whitewater, A.L. Melander (USNM). Alameda Co., 1 ♂, Sunol, W.W. Wirth (USNM). Inyo Co., 1 ♂, Surprise Canyon, R.O. Schuster (CIS). Nevada Co., 1 ♂, Sagehen Cr, nr Hobart Mills, C.N. Slobodchikoff (CAS). Riverside Co., 3 ♂♂, P.L. Boyd Desert Research Center, Saul I. Frommer, L. LePre; 1 ♂, Horsethief Cr, 10 mi S Palm Desert, L. LaPre; 1 ♂, Desert Hot Springs (UCR); 1 ♂, 1000 Palms Canyon, P.A. Rausch (UCR). San Bernardino Co., 1 ♂, Mill Cr, Thurman Flats, P.A. Rausch (UCR). Santa Clara Co., 2 ♂♂, Coyote Creek, R. Whitsel (JES). Shasta Co., 118 ♂♂, Fall River Mills; 1 ♂, Hat Creek, Pitt R, C. Apperson (BYU, CAS, INHS, KU, JES, UCR, USNM). Sonoma Co., 1 ♂, Triniti, N.W. Frazier (CAS). Tehama Co., 2 ♂♂, Red Bluff (CAS). Tulare Co., 1 ♂, E Success Res, T.W. Fisher (UCR).

CO: Chaffee Co., 18 ♂♂, Arkansas R, Rd 301, Fisherman's Br, 2338 m elev, T15S, R78W, S3; 40 ♂♂, 6 ♀♀, Sand Lake Br, Salida, 2143 m elev, T50N, R9E, S31, Chalk Cr; 1 ♂, Hwy 285, 2338 m elev, T15S, R77W, S14. Fremont Co., 12 ♂♂, 1 P & ♂, Arkansas R, Howard Br, 2033 m elev; 22 ♂♂, Parkdale Siding Br, 1747 m elev, T18S, R72W, S13; 17 ♂♂, Hwy 115, 9th St Br, Canyon City, 1618 m elev, T85S, R70W, S33; 9 ♂♂, Texas Cr Br, 1879 m elev, T19S, R73W, S7; 21 ♂♂, Portland Br, 1535 m elev, T19S, R68W, S17/20. Lake Co., 1 ♂, Arkansas R, upstream from Lake Cr inflow, 2748 m elev, T11S, R80W, S24. Pueblo Co., 1 ♂, Arkansas R, Hobson Ranch, 1504 m elev, T20S, R67W, S6; 6 ♂♂, Stilling Basin Br, 1444 masl, T20S, R66W, S36, all (except as indicated) collected by S.J. Herrmann (AEI, CAS, JES, UMN, USNM).

NM: Rio Arriba Co., 1 ♂, Chama R, 2 mi S Chama, Doles and Milensky; 1 ♂, Chama R below El Vado Dam, Doles and Milensky (JES).

This species is dedicated to Dr. Scott J. Herrmann, University of Southern Colorado, who collected a significant part of the type series from the Arkansas River in Colorado.

Cricotopus (*Cricotopus*) *infuscatus* (Malloch)

Orthocladius infuscatus Malloch 1915:517; type locality, Peoria, IL.

Cricotopus (*Cricotopus*) *infuscatus* (Malloch); Sublette and Sublette 1979:69, distribution, synonymy; LeSage and Harrison 1980a:81 and Fig. 10, adults, immatures, distribution; 1980b:376, ecology; 1980c:2. biology of parasites; Oliver et al. 1990:23, catalog, synonymy.

Cricotopus edurus Sublette & Sublette 1971:85; type locality, P.L. Boyd Desert Research Center, near Palm Desert, Riverside Co., CA. *New synonym.*

Cricotopus subfuscus Sublette & Sublette 1971:98; type locality, Hat Creek, Fall River Mills, Shasta Co., CA. *New synonym.*

Cricotopus infuscatus (Malloch); Boesel 1983:83, distribution, synonymy.

DIAGNOSIS.—The sharply defined basidorsal and basiventral lobes of the gonocoxite which are about of equal length, the basidorsal lobe which bears about 6–8 main setae (Sublette and Sublette 1971: Figs. 6, 35; LeSage and Harrison 1980a: Fig. 10), and the abdominal chaetotaxy (Sublette and Sublette 1971: Figs. 5, 34), together with the color pattern (Sublette and Sublette 1971: Figs. 1, 2), separate this species from other Nearctic *Cricotopus*. The larva and pupa have been characterized by LeSage and Harrison (1980a:84); both stages are similar to those of *C. (Cricotopus) annulator* (Goetghebuer), described above. The pupa differs in usually lacking the apical shagreen band on T II and having a higher number of recurved hooks on T II (63–112). The number of recurved hooks on T II is quite variable, with eastern populations generally having a higher number. The larva has a strongly crenulate mandible, which is in contrast to that of *C. annulator* with its virtually smooth outer mandibular margin.

Discussion.—Additional material of *C. infuscatus* indicates a much broader range of color variation and chaetotaxy than was previously known, hence the synonymies given above.

Ecology.—Lenat and Folley (1983) demonstrated a bimodal pattern of adult emergence for adults in the *infuscatus*-group. LeSage and Harrison (1980b) reported that *C. infuscatus* could tolerate pollution, 80% of the populations occurred in riffles, most emergences were at temperatures of 16–21°C, and swarming occurred over grass clumps or the ground at less than 1 m in height at 7–11 m from the stream margin. Ruse et al. (unpublished data) collected adults from the upper Arkansas River in Colorado at elevations ranging from 1431 to 2748 m.

Distribution.—Widely dispersed throughout lower elevations and latitudes of North America.

Material examined.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 3 ♂♂, river mi 61.5, 826 m elev; 1 ♂, river mi 63.7, 818 m elev; 1 ♂, river mi 164.5, 533 m elev; 2 ♂♂, river mi 166.5, 532 m elev. Other material: Adults have been examined from throughout most of the range of this species in North America, including extensive reared series from South Dakota and New Mexico.

Cricotopus (Cricotopus) *trifascia* Edwards

Cricotopus trifascia Edwards 1929:322, male. Type locality, England; Boesel 1983:84, distribution.

Cricotopus (Cricotopus) trifascia Edwards; Hirvenoja 1973:244, adults, pupa, larva, review, distribution; Sublette and Sublette 1979:70; synonymy, distribution; Laville 1979:160 and Wilson 1987:391, ecology; LeSage and Harrison 1980a:102, distribution, synonymy; 1980b:376, ecology; 1980c:2, biology of parasites; Lenat and Folley 1983:152, phenology, distribution; Mason and Lehmkuhl 1983:196, 1985:877, distribution, phenology; Simpson et al. 1983:4, distribution, adults, pupa, larva, in key (after Hirvenoja 1973); Hudson et al. 1990:9, in list, distribution; Oliver et al. 1990:24, distribution, synonymy; Langton 1991:208, pupa.

Diagnosis and discussion.—This is the only Nearctic species of *Cricotopus* that lacks a basidorsal gonocoxite lobe. The pupa has the distinctive features of heavy shagreen on terga VII and VIII as well as 2 large and 1 small macrosetae on the anal lobe.

Ecology.—*Cricotopus trifascia* is usually in rapidly flowing waters ranging from 1st-order streams to large rivers (Simpson and Bode 1980). In small streams in England it has been taken on gravel or *Ranunculus* (Pinder 1980, Pinder and Farr 1987). Mason and Lehmkuhl (1983) reported 3 peaks of adult emergence upstream from an impoundment: spring, midsummer, and fall. However, highest numbers were found 23 km downstream from the impoundment and with a unimodal, midsummer emergence about a month after the upstream populations. In Germany, Kownacki and Margreiter-Kownacka (1993) reported *C. trifascia* as occurring more commonly in the lower stretches of the Alz River rather than immediately below a lake outflow; in the Fulda, Lehmann (1971) found this species rather widely distributed, occurring in the metarhithral to the potomal regions in moderately strong current. The species was the dominant form in a small, heavily polluted stream in southern Ontario, absent from another polluted stream, but clearly rheophilous with at least 80% of the populations in riffles of cobble and pebbles densely covered by diatoms and filamentous algae; adult emergences occurred at water temperatures of 16–21°C, with adult male swarms 2–3 m aboveground where tree branches were used as lateral swarm markers (LeSage and Harrison 1980b). In an organically enriched small chalk stream in southern England this species occurred in low numbers only at an unpolluted station (Pinder and Farr 1987). The larval tubes of *C. trifascia* are constructed largely of detritus and filamentous algae or filamentous algae alone, and the stream in which stones occurred had a thin aufwuchs film except during summer, at which time large areas of stones had a *Cladophora* blanket (Brennan and McLachlan 1979). The species has been reported from periphyton in a large stream, the Danube, associated primarily with *Cladophora* (Janković 1973). It has been taken in low numbers from 2 of 5 stations receiving organic enrichment in the River Sar in Spain (Cobo and Gonzáles 1991). In Lebanon, *C. trifascia* occurred at 800–1200 m at several different stream sites, most of which had mosses or macrophytes; 1 station was polluted (Moubayed and Laville 1983). A population in a 3rd-order trout stream consisted of 2 cohorts that made up 9.7% of total secondary production of midges (Berg and Hellenthal 1992a, 1992b). The species, collected at a station with medium levels of zinc, was considered to be tolerant according to the pollution tolerance codes developed by Wilson and McGill (1982) (Armitage and Blackburn 1985). In New Mexico, *C. trifascia* was an uncommon species, occurring in the San Juan River, an upper tributary of the Colorado River, and in the upper Rio Grande (Sublette and Sublette 1979). Adults have been taken from the upper Arkansas River in Colorado at elevations ranging from 1431 to 2748 m elevation (Ruse et al. unpublished data).

DISTRIBUTION.—Saskatchewan to Ontario and New York, south to California, New Mexico, and North Carolina.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 2 ♂P, 1 L, river mi 0.0, 947 m elev; 2 ♂♂, river mi 53.0, 847 m elev; 3 ♂♂, river mi 61.5, 826 m elev; 1 ♂P, river mi 74.3, 792 m elev; 1 ♂, river mi 98.0, 732 m elev; 1 Pex, river mi 151.2, 556 m elev. Other material: Specimens have been examined from throughout the range of this species, including extensive reared material from New Mexico.

Eudactylocladius dubitatus
(Johannsen)

Orthocladius (Dactylocladius) dubitatus Johannsen 1942:72; type locality, NY.

Hydrobaenus dubitatus (Johannsen); Roback 1957:76, immature stages.

Orthocladius (Eudactylocladius) dubitatus Johannsen; Sublette 1967:507, review; Hudson et al. 1990:11, in list, distribution; Oliver et al. 1990:31, in catalog.

Eudactylocladius dubitatus (Johannsen); Sublette and Sublette 1979:73, generic position, distribution.

DIAGNOSIS AND DISCUSSION.—The males of this genus can be separated from the closely related *Orthocladius* (s.s.) by the greatly reduced basidorsal and basiventral gonocoxite lobes. The pupa has distinctive paired spinulae patches on terga II or III–VI, lacks recurved hooks on tergum II, and has a short, smooth, saclike thoracic horn that arises from a short stalk. The male of *E. dubitatus* can be separated from other Holarctic species by its short anal point, basimedian gonocoxite lobes that are not produced, and an apically tapered gonostylus with a scarcely discernible dorsodistal carina (cf. Sublette 1967:505, Fig. 17). The pupa has been redescribed by Roback (1957:81: Figs. 194–196). Our material suggests that this species is more variable in the pupal stage than heretofore known: the weak, paired shagreen patches of tergum II may be reduced to just a few points, or even completely absent; the apical spinulae row on tergum VIII, in like manner, may be well developed, reduced to a few points, or even absent. A unique feature appears to be the presence of well-developed pedes spurii B on terga I, II, and III.

ECOLOGY.—*Eudactylocladius dubitatus* is probably madicolous since the pupae are sometimes taken in streams. The madicolous biotope occurs as a thin film of water on any solid substratum such as seeps on vertical rock faces, splash zones of rapids and waterfalls, water interface of emergent vegetation, and at stream margins. Spring runs provide a stable environment and will usually include members of this assemblage. The species, while rare in this system, has been collected on the upper Arkansas River of Colorado at elevations ranging from 1444 to 2143 m (Ruse et al. unpublished data). Species of this genus occur in lakes, temporary ponds, swamps, and in madicolous assemblages on rock faces and in moist soil (Cranston et al. 1989).

DISTRIBUTION.—California to New Mexico east to New York and Pennsylvania.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 2 Pex, river mi 124.6L, 625 m elev, 26-XI-91. Other material examined: reared specimens from California, Colorado, and New Mexico.

Eukiefferiella claripennis
(Lundbeck)

Chironomus claripennis Lundbeck 1898:281; type locality, Greenland.

Eukiefferiella claripennis (Lundbeck); Oliver 1970: 102, lectotype; Lehmann 1972:359, adult, pupa, distribution, synonymy; Pinder 1974:198, Laville 1979:160, Wilson 1987:391 and 1989:373, ecology; Halvorsen 1981:34, review, female; Hudson et al. 1990:9, Oliver et al. 1990:26, catalog, distribution, synonymy; Langton 1991:125, pupa.

DIAGNOSIS AND DISCUSSION.—The adult male is characterized by having bare eyes, an absence of R_{2+3}, a moderately extended costa that ends slightly proximal to apex of M_{3+4} (Lehmann 1972: Fig.7), and, above all, the features of the male genitalia (Lehmann 1972: Fig. 6). The pupa has a distinctive thoracic horn and abdominal chaetotaxy (Lehmann 1972: Figs. 8, 9). The adult is very similar to *E. brevinervis* (Malloch) (Sublette 1970:71) but differs in having a lower antennal ratio (0.75–1.30; *E. brevinervis*, 2.0–2.4).

ECOLOGY.—*Eukiefferiella claripennis* is widely distributed in lower and medium elevation streams. It is eurythermous and rheobiontic (Lehmann 1972). Pinder (1980), Pinder and Farr (1987), and Pinder et al. (1987) collected it most often on *Ranunculus* and gravel substrates, while Ringe (1974), Halvorsen (1981), and Nolte (1991) reported it as an inhabitant of aquatic mosses. Halvorsen (1981) also found it on the surface of rocks in swiftly flowing water at 500 m elevation, and Millet et al. (1987) reported it from rocks with *Cladophora*. *E. claripennis* tolerates low to medium levels of zinc and is considered to be relatively tolerant according to the pollution codes of Wilson and McGill (1982) (Armitage and Blackburn 1985). Gower et al. (1994) reported this to be one of the most abundant and tolerant chironomids, occurring at stream stations with high levels of copper and aluminum. Pinder and Farr (1987) collected it from stations with elevated levels of organic enrichment in a small chalk stream in southern England, but not in numbers greater than at clean water stations. It has been taken from a calcareous stream with elevated levels of zinc but not from acid streams with higher levels of zinc (Wilson 1988), and is considered to be a moderately pollution-tolerant species (Bazerque et al. 1989). In Lebanon, Moubayed and Laville (1983) reported this species from a seasonal limnocrene in eddies at the outflow, with water temperatures ranging from 14° to 16°C; elevation was 850 m. Oliver and Sinclair (1989) regarded it as a member of the madicolous assemblage. According to Bode (1983), the *claripennis*-group is the most tolerant member of the genus, occurring from high-altitude streams to larger, warmer rivers. In the brown-water stream system studied by Boerger (1981) in Alberta, *E. claripennis* constituted only 0.5% of the Orthocladiinae males/m^2/yr. It is one of the predominant chironomids that emerged in the spring from the River Pang in England (Ruse 1992). Ringe (1974) observed 4 adult emergence periods from a small stream in central Germany, with most individuals emerging during the interval from June to August. In Austria, Schmid (1993) found low larval densities of this midge from a coldwater, gravel-bottomed stream. In Germany it has been reported from the Danube, a large river (Anderwald et al. 1991), as well as a regulated, primary tributary, the lower Inn River (Reiss and Kohmann 1982); in the Alz River this species avoids the soft sediments immediately below a lake outflow but is common farther downstream (Kownacki and Margreiter-Kownacka 1993). In the French Pyrenees the streams of the Ossau Valley support moderate numbers of *E. claripennis* at elevations from 500 to 800 m, in slow- to fast-moving water; maximum temperatures range from 15° to 18°C (Laville and Vinçon 1991). Ruse et al. (unpublished data) collected adults of this species at elevations ranging from 1431 to 2969 m in the upper Arkansas River in Colorado, from areas where substrata range from boulder-cobble to gravel-sand. In New Mexico *E. claripennis* occurs in all northern and western drainages in cool to cold waters where substrata are predominantly gravel-sand (Sublette and Sublette 1979).

Steep rock faces at or near the water's edge in Grand Canyon, together with the occasional patches of cobble-gravel, provide considerable madicolous habitat and are the probable preferred habitat.

DISTRIBUTION.—Holarctic; widely distributed in the Nearctic region; introduced into Hawaii (Oliver et al. 1990).

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 4 ♂♂, river mi 0.0, 947 m elev; 1 ♀ Pex, river mi 3.4, 945 m elev; 4 ♂♂, river mi 31.5, 876 m elev; 1 ♂, river mi 31.8, 876 m elev; 1 ♀ Pex, river mi 34.1, 872 m elev; 1 ♂, river mi 43.2, 861 m elev; 1 ♂, river mi 61.5, 826 m elev; 2 ♂♂, river mi 65.3, 808 m elev; 1 ♂, river mi 98.0, 706 m elev; 2 ♂♂, river mi 108.5, 664 m elev; 3 ♂♂, river mi 133.0, 597 m elev; 1 ♂, river mi 150.0, 556 m elev; 1 ♂, river mi 172.0, 521 m elev; 1 ♂, river mi 204.0, 454 m elev; 1 ♂, 1 ♀ Pex, river mi 205.7, 451 m elev.

Eukiefferiella coerulescens (Kieffer)

Trichocladius coerulescens Kieffer, in Zavřel 1926:279.

Spaniotoma (*Eukiefferiella*) *coerulescens* (Kieffer); Edwards 1929:354, generic (subgeneric) position, review, distribution.

Eukiefferiella coerulescens (Kieffer): Brundin 1956:87, male, in key, generic position, distribution; Lehmann 1972:369, male, pupa; Hudson et al. 1990:9, in list, distribution; Langton 1991:124, pupa.

DIAGNOSIS.—In the adult the presence of distinct microtrichia between the eye facets and a bare squama are unique features among Nearctic *Eukiefferiella*. The pupa has a distinctive chaetotaxy as well as very short anal macrosetae, of which 1 is distinctly shorter than the other 2 (cf. Langton 1991: Figs. 51a–c).

DISCUSSION.—Nearctic material of adults and pupae agrees well with the descriptions given by Lehmann (1972:369) except that the antennal ratio of the male is intermediate between that given for this species and *E. boevrensis* Brundin. Langton (1991:124) has redescribed the pupa (in a correction sheet he has added that the pupa has a small, thin-walled, saclike thoracic horn; this is very frequently lost and thus in earlier descriptions was described as lacking). Our material agrees well with his description.

ECOLOGY.—Listed as a member of the madicolous assemblage by Oliver and Sinclair (1989) (see *Eudactylocladius dubitatus*, above), *E. coerulescens* has also been taken from aquatic mosses (Ringe 1974, Laville and Lavandier 1977, Nolte 1991) and has been found in streams with organic enrichment (Cobo and Gonzáles 1991). Bode (1983) reported the *coerulescens*-group as apparently widespread in North America, occurring mostly in small to medium-sized, unpolluted streams. Schmid (1993) collected it in low numbers from the surface and gravel interstices of a coldwater, gravel-bottomed stream in Austria. In Germany, Ringe (1974) observed that adult emergence in 2 small streams was essentially bivoltine but that the peaks of emergence were out of phase between the 2 streams, with the warmer stream having the main peaks of emergence almost a month before the stream with the colder, more uniform temperatures. In the Fulda, Lehmann (1971) found this species only in strongly flowing water in moss or on stones of the krenal to hyporithral regions. Kownacki (1982) found this species at only a single station in a small upland stream in Poland, occurring in an area of low current. Mouyabed and Laville (1983) reported this species in Lebanon from 3 stream systems at elevations above 1100 m, usually on moss- or algal-covered rubble. In the Ossau Valley of the French Pyrenees, *E. coerulescens* is one of the more abundant species, occurring most often in fast to very fast streams from 500 to 2100 m elevation; maximum temperatures range from 10° to 15°C (Laville and Vinçon 1991). One of the most unusual occurrences of *E. coerulescens* was reported in an underground stream of a cave system in Rumania some 8000 m from its epigyean source (Albu and Stergar 1971). Adults have been taken in the Arkansas River of Colorado at elevations ranging from 1431 to 1618 m, primarily from gravel-sand substrata (Ruse et al. unpublished data). In New Mexico *E. coerulescens* is found mostly in the cool to cold northern and western streams where gravel-sand substrata predominate; a record from the warm-water, lower Pecos River was from a gravel substratum (Sublette unpublished data).

DISTRIBUTION.—Holarctic; this species is probably more widely distributed in the Nearctic region than records indicate.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♀ P, river mi 0.0, 947 m elev; 1 ♂, river mi 3.4, 941 m elev; 1 ♂, river mi 31.5, 876 m elev; 2 ♂♂, river mi 43.2, 861 m elev; 1 ♂, river mi 68.0, 808 m elev. In addition, we have reared material from Arizona, Colorado, and New Mexico.

Eukiefferiella ilkleyensis (Edwards)

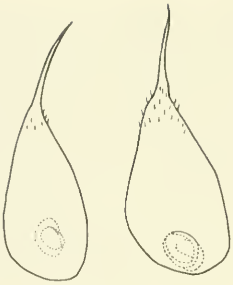
(Figs. 36–39)

Spaniotoma ilkleyensis Edwards 1929:349; type locality, Ilkley, Yorkshire, England.

Eukiefferiella ilkleyensis (Edwards); Lehmann 1972:372, revision, adult, pupa; Pinder 1974:198 and Laville 1979: 161, ecology; Storey 1987:339, developmental ecology; Hudson et al. 1990:9, in list, distribution.

Nearctic males and pupae, which are considered here as conspecific with Palearctic populations, differ in some slight details. The following descriptions define the Nearctic material.

MALE.—*Coloration*: Almost entirely blackish brown; scutellum, humeral and pleural areas yellowish; legs dark; abdomen blackish brown with the narrow apices of T VII and VIII somewhat paler; genitalia dark. Antenna with 13 flagellomeres. Antennal ratio 0.85–1.05 (10). Palpal proportions 62:101:101:164 µm. Eyes reniform, without dorsal extensions; ocular ratio 0.68–0.73 (4). Clypeus rectangular, much wider than long, slightly narrower at



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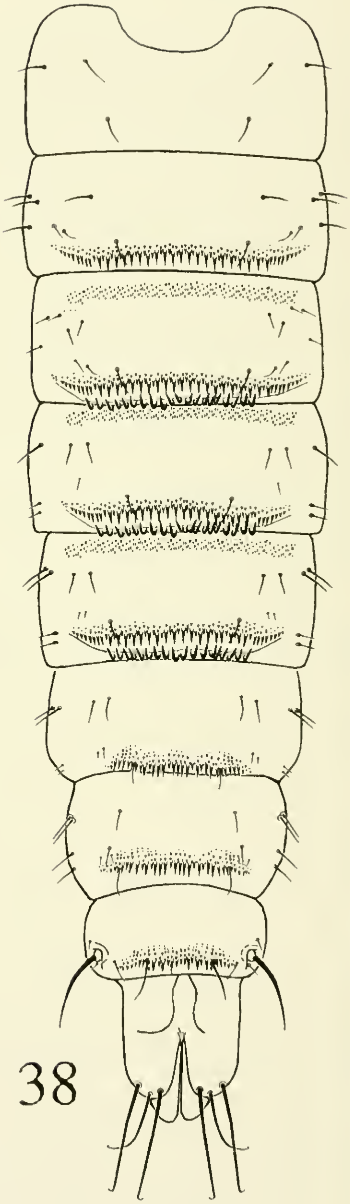

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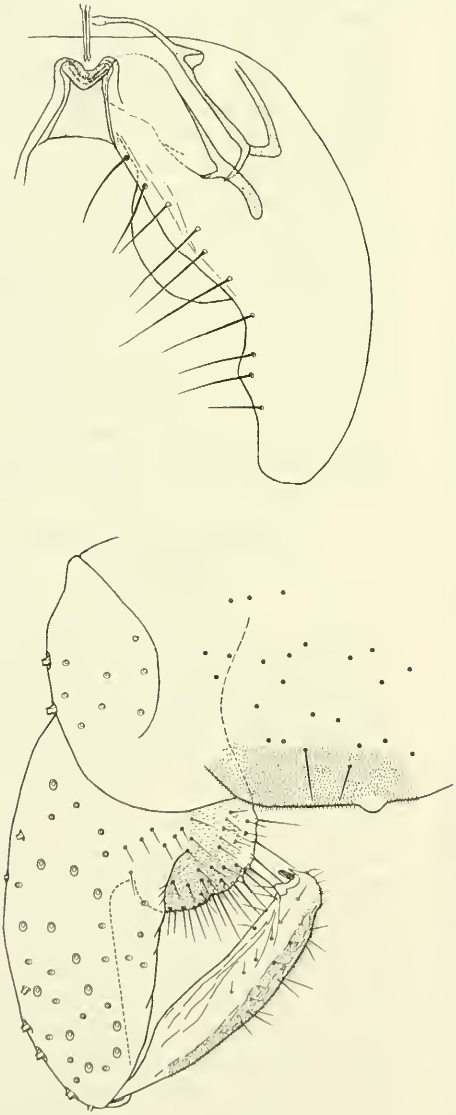

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Figs. 37–39. *Eukiefferiella ilkleyensis*. Pupa: 37, thoracic horn; 38, abdominal shagreen and chaetotaxy. *Metriocnemus stevensi*. Male: 39, genitalia (dorsal view below, internal skeleton above).

base than width of the antennal pedicel; clyp/ped ratio 0.87–0.93 (9); clypeus with 6–8 (12) setae. Temporal setae 2–5 (12), usually in a small clump behind dorsal apex of the eye (with 1–2 very fine inner verticals observed in 2 specimens).

Thorax: Antepronotum slightly and almost evenly tapered to the apex, collarlike. Thoracic chaetotaxy: lateral antepronotals 2–5 (5); dorsocentrals 8–12 (5), set in paler alveoli, in a single row; acrostichials 7–13 (5), mostly in 2 rows; prealars 3 (5); supra-alars lacking; scutellars 7–11 (5), mostly in a staggered single row.

Wing: Membrane with very fine microtrichia barely visible at phase 500X. Costa extended 30–55 (6) µm beyond R_{4+5}, which ends distinctly proximal to tip of M_{3+4}. R_{2+3} ends at 0.29–0.35 (5) of the distance between apex of R_1 and R_{4+5}. Venarum ratio 1.09–1.17 (5). Wing length 1.90–2.37 (9) mm. Squama with 6–13 (11) marginal setae. Wing vein setae: R 1–4 (5), R_1 0–1 (5), other veins without setae.

Legs: All legs with a single tibial spur; foretibial spur length 48–58 (5) µm; middle tibial spur length 38–46 (5) µm; hind tibial spur length 54–70 (5) µm. Pulvilli absent. Leg ratios: P I 0.60–0.66 (10); P II 0.48–0.55 (5); P III 0.57–0.61 (5). P III comb setae 12–14 (5). P II and P III sensilla chaetica lacking.

Abdomen: Setae on terga II–IV broadly strewn over most of each tergum except for a posteromedian concave area devoid of setae; terga V–VIII with setae strewn over most of each tergum except for a narrow apical transverse band.

Genitalia (Fig. 36): Ninth tergum with 2–3 (10) setae. Virga absent. Gc/Gs ratio 1.80–2.06 (5).

PUPA.—*Exuviae*: Exuviae almost entirely brown.

Cephalothorax: Frontal setae absent. Thoracic horn (Fig. 37), length 122–152 µm; apical denticles on the basal enlargement very weak or perhaps absent in some specimens. Cephalothorax almost smooth on either side of median suture. Precorneal setae with 1 long and 2 smaller setae. Dorsocentrals small, almost in a line, $Dc_{1,3}$ larger, $Dc_{2,4}$ smaller. Wing sheaths without bacatiform papillae or nasiform tubercles.

Abdomen: Abdomen length 1.59–1.90 mm. Shagreen pattern and chaetotaxy (Fig. 38). Pedes spurii B lacking. Terga II–VIII with posterior spines; T III–V with a continuous row of recurved hooks behind the spine row; hook number: III 17–24, IV 18–24, V 12–18. Sterna VI and VII with inconspicuous apical denticles. Tergum VIII with $L_{1,2,4}$ very fine; L_3 larger and heavier but not spinose. Anal macrosetae of unequal length, with the medial 1 smaller than the lateral 2; lateral macrosetal length 124–150 µm.

DIAGNOSIS AND DISCUSSION.—Despite some minor differences, this population is considered to be conspecific with the Palearctic *E. ilkleyensis* (Edwards) and is very similar to the Holarctic *E. devonica* (Edwards) in adult and pupal stages. The adult differs in having the ventral junction of the gonocoxites irregularly papillose and the apex of the phallopodeme weakly digitate (not always clearly visible, being dependent upon the orientation of the genitalia on the slide), while both Palearctic *E. ilkleyensis* and *E. devonica* have a smoothly rounded medial junction and the phallopodeme is not illustrated as digitate (cf. Lehmann 1972: Figs. 30, 34). Further, the temporal setae of this population are usually restricted to behind the dorsal apex of the eye while Palearctic *E. ilkleyensis* has a group of 3–4 setae near the midline in addition to the group behind the dorsal apex of the eye (cf. Lehmann 1972: Fig. 36). The antennal ratio is much higher than in *E. devonica*.

The pupa of this species can best be distinguished by the different thoracic horn. In Palearctic *E. ilkleyensis* the filament is short (cf. Lehmann 1972: Fig. 37) to very short (cf. Langton 1991: Fig. 51d), while in this population the filament is distinctly longer; further, the fine denticles at the base of the filament are usually distinct in *E. ilkleyensis*, whereas in this population the denticles are very sparse (visible only at phase 500X) or entirely absent. Although the thoracic horn is nearer to that illustrated for *E. devonica* (Lehmann 1972: Fig. 32), the filament, which is shorter than in that species, and the absence of apical hooks on sternum VIII clearly distinguish this species from *E. devonica*.

ECOLOGY.—*Eukiefferiella ilkleyensis* is a member of the *devonica*-group, which is associated with mosses and algae in small to large rivers (Bode 1983). It has been found most often on *Ranunculus* (Pinder 1980), *Ranunculus* and gravel (Pinder et al. 1987), or aquatic mosses (Ringe 1974, Nolte 1991). Armitage and Blackburn (1985) reported the species at stream sites with low zinc concentrations and considered it to be intolerant in the pollution tolerance codes of Wilson and McGill (1982). However, Cobo and Gonzáles (1991) collected it on the Sar River in Spain at 1 station of 5 that received organic enrichment. Pinder and Farr (1987) also reported it in low numbers from a small chalk stream in southern England at a station with elevated levels of organic enrichment. In Poland in the River San, Kownacki (1989) found this species to be one of the dominants above a sewage outfall, but it diminished or disappeared at downstream stations. Storey (1987) considered *E. ilkleyensis* to be a scraper/herbivore that selectively feeds on aufwuchs, especially epiphytic diatoms. Tokeshi and Townsend (1987) described aspects of the ecology of a population living epiphytically on *Myriophyllum spicatum* L. in a small river in eastern England. It was collected by Schmid (1993) from a coldwater, gravel-bottomed stream in Austria; larval densities were low. Kownacki and Kownacka (1971) and Kownacki (1982) found this species at several stations on small upland streams in Poland; however, greatest numbers were reported over stony bottoms. Kownacki and Zosidze (1980) and Kownacki (1985) also reported it from medium to large, stony streams from the Little Caucasus Mountains of Georgia (Adzhar) and the Caucasus Mountains of Azerbaijan. In the Alz River of Germany, Kownacki and Margreiter-Kownacka (1993) reported that this species avoids slower currents and softer bottoms below a lake outflow but occurs commonly in lower stretches of the stream. In Lebanon, Moubayed and Laville (1983) reported *E. ilkleyensis* at only 1 station on the Assi River, in fast current, on rubble partially covered with mosses. In the Ossau Valley of the French Pyrenees, this is a rare species occurring in fast to slow streams at elevations of 450–500 m; maximum temperature is 15°C (Laville and Vinçon 1991). Ruse et al. (unpublished data) found it at only a single location in the upper Arkansas River of Colorado at an elevation of 1431 m.

DISTRIBUTION.—We have reared material from streams in Arizona, Colorado, and New Mexico.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 2 ♂♂, 5 ♂P, 5 ♀ Pex, river mi 3.4, 941 m elev; 1 ♂ Pex, 1 ♀ Pex, river mi 34.1, 872 m elev; 1 Pex, river mi 63.7, 818 m elev; 1 ♂P, river mi 74.3, 792 m elev; 1 ♂, river mi 75.3, 785 m elev; 1 ♂, river mi 0.0, 947 m elev; 1 ♂, river mi 52.7, 846 m elev; 2 ♂♂, river mi 71.0, 808 m elev; 2 ♂♂, river mi 72.0, 796 m elev; 1 ♂, river mi 87.5, 740 m elev; 1 ♂, river mi 88.0, 739 m elev; 1 ♂, river mi 89.0, 736 m elev (CAS, USNM, CNC, INHS, JES).

Eukiefferiella sp.

DIAGNOSIS, DISCUSSION, AND ECOLOGY.—The adult is scarcely distinguishable from that of *E. ilkleyensis* in genitalic features; however, the tip of the antenna is broken off (antennal ratio estimated to be about 1.0). The pupa is readily distinguishable by its distinctive thoracic horn, which is more like that of *E. devonica* (Edwards) (Lehmann 1972: Fig. 32). Unfortunately, the presence of small hooks at the apex of S VII (Lehmann 1972: Fig. 33) cannot be ascertained, as the apex of the associated pupal exuviae is missing beyond segment V.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂ Pex, river mi 63.7, 818 m elev.

Limnophyes sp.

DIAGNOSIS AND DISCUSSION.—A single male was taken, but during slide preparation the genitalia were badly crushed, hence the lack of a specific determination.

ECOLOGY.—The genus *Limnophyes* occurs in numerous ecotopes, ranging from aquatic (particularly madicolous) to semiterrestrial habitats.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 133.5, 600 m elev, 9-11-90.

Metriocnemus stevensi
Sublette, new species

HOLOTYPE MALE.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, Vaseys Paradise, river mi 31.8, 876 m elev, J.S. (CAS).

Coloration: Head, thoracic vittae, preepisternum, and postnotum blackish brown; antepronotum and scutellum paler than postnotum; humeral and pleural areas yellowish; legs and abdomen dark brown.

Head: Antenna with 13 flagellomeres; fully plumed. Antennal ratio 0.93. Palpal proportions 47:195:172:211 µm. Eyes with dorsal extension short and wedge-shaped. Ocular ratio

0.45. Clypeus quadrangular, slightly wider at base than width of the antennal pedicel (1.07); with 22 (23; 1) setae. Temporal setae 23 (31; 1), those in the postocular series coarse and in a single row, while those lying medial to the eye finer, multiserial, and reaching to near midline of the head.

Thorax: Antepronotum rather broad and collarlike, almost parallel-sided in the apical half. Thoracic chaetotaxy: lateral antepronotals 7 (9; 1); dorsocentrals 53 (42; 1) (including 15 [16; 1] humerals), in 3 staggered rows posteriorly, with the humerals becoming multiserial anteriorly; acrostichials about 35 (37; 1), partially in 2 rows; prealars 18 (23; 1); supra-alars 2 (2; 1); scutellars 32 (32; 1), in a single row laterally, becoming 3–4 rows medially; preepisternals 9 (5; 1).

Wing: Membrane with fine macrotrichia over most of the membrane. Costa extended 170 (126; 1) μm beyond R_{4+5}, which ends slightly distal to M_{3+4} at 0.21 of the distance between apex of M_{3+4} and M_{1+2}. R_{2+3} almost parallel to R_1, ending at 0.14 of the distance between its apex and apex of R_{4+5}. Venarum ratio 1.24 (1.23; 1). Wing length 2.25 (1.92; 1) mm. Squama with 17 (19; 1) marginal setae. Wing vein setae: R 75, r-m 7, R_1 67, R_{4+5} 128, M 24, M_{1+2} 104, M_{3+4} 24, Cu 32, Cu_1 18, remigium 6.

Legs: Foretibial spur of holotype broken at tip (54; 1) μm; middle tibial spur lengths 31/31 (34/28; 1) μm (tip of longer spur on holotype broken); hind tibial spur lengths 53/28 (72/34; 1) μm (extreme tip of longer spur on holotype broken). Pulvilli vestigial. Tarsal pseudospurs present on Ta_{1-3} of P II and P III (P III tarsi missing on holotype). Leg ratios: P I 0.63; P II 0.43 (0.40; 1); P III (0.44; 1) (P III lacking on holotype). P III comb setae 11 (12; 1). P II and P III sensilla chaetica lacking (P III tarsi missing on holotype).

Abdomen: Abdominal terga with scattered setae; T IV with about 93 setae; sterna III–VI with a midventral row of setae, that of S III uniserial, S IV 2X with S V–VI multiserial; S II–VI with multiserial laterals; S VII–VIII with medial and lateral setal bands fused.

Genitalia (Fig. 39): Ninth tergum with 24 (21; 1) setae. Small virga present; length 24 μm. Gc/Gs ratio 1.78.

DIAGNOSIS AND DISCUSSION.—The combination of heavily haired wings, presence of preepisternal setae, and extremely short anal point is unique among Nearctic *Metriocnemus*.

ECOLOGY.—The genus *Metriocnemus* occurs in a wide variety of habitats, from madicolous to semiterrestrial habitats.

MATERIAL EXAMINED.—Paratype (and holotype) ♂, AZ: Coconino Co., Grand Canyon National Park, Colorado River, mi 31.8, 876 m elev, LES (CAS).

This species is dedicated to Dr. Lawrence E. Stevens who initiated and coordinated this study.

Orthocladius (Euorthocladius) luteipes Goetghebuer

Orthocladius luteipes Goetghebuer 1938:457; type locality, Austria.

Orthocladius (Euorthocladius) luteipes Goetghebuer; Soponis 1990:23, revision, adults and immatures, distribution.

DIAGNOSIS AND DISCUSSION.—The adult male and immatures have been separated in key by Soponis (1990). Males are similar to those of *Orthocladius (Euorthocladius) rivicola* Kieffer but may be recognized by the more square-shaped basidorsal gonocoxite lobe below which the basiventral gonocoxite lobe is more weakly projecting than in *O. rivicola*; however, the pupae are more distinctive than the adults. It is probable that some males identified in the literature as *O. rivicola* are actually *O. luteipes*.

DISTRIBUTION.—Palearctic; Oregon to New York, south to Arizona and Georgia.

ECOLOGY.—*Orthocladius luteipes* occurs in creek and riverine habitats, spinning gelatinous cases on stones. This species' distribution broadly overlaps that of *O. rivicola*.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 3.4, 941 m elev, 24-VII-71.

Orthocladius (Euorthocladius) rivicola Kieffer

Orthocladius rivicola Kieffer 1911:181; type locality, Germany.

Orthocladius (Euorthocladius) rivicola Kieffer; Laville 1979:161, ecology; Soponis 1990:26, revision, all stages, distribution; Hudson et al. 1990:11, in list, distribution; Oliver et al. 1990:31, catalog, distribution.

DIAGNOSIS AND DISCUSSION.—Soponis (1990) has differentiated the adult and pupa of this species from other Holarctic members of the subgenus.

ECOLOGY.—*Orthocladius rivicola* has been categorized as "less pollution resistant" (Bazerque et al. 1989), although Cobo and Gonzáles

(1991) reported it at 3 of 5 stations receiving organic enrichment on the River Sar in Spain. In the high arctic Hayes and Murray (1987) found this to be one of the numerically dominant forms that exhibited a bimodal emergence during a 24-h study, with emergence continuing over the entire 6-wk study period. Laville and Lavandier (1977) also reported this as a numerically dominant species all along the length of a torrential brook in the Vallon d'Estaragne in the French Pyrenees. In the Ossau Valley of the French Pyrenees this was one of the "frequent or abundant" species in fast to very fast waters at elevations of 500–1500 m; maximum water temperatures were 12–15°C (Laville and Vinçon 1991). It has been reported from aquatic mosses (Kownacki 1971, Nolte 1991) and from *Cladophora* in the aufwuchs assemblage (Janković 1973). Mason and Lehmkuhl (1983) observed that numbers of this species were not diminished downstream from a dam when compared with upstream populations. In Austria, Schmid (1993) collected larvae in low numbers from the surface and gravel interstices in a coldwater stream, while Anderwald et al. (1991) took it from the Danube, a large river. It has also been reported from the lower Danube in the former Yugoslavia (Janković 1973). Ringe (1974) illustrated an emergence period from April to August in a small stream in central Germany, with 1 major peak of emergence occurring in early May; in the Fulda, Lehmann (1971) reported the highest abundance of this species in the strongly flowing currents of the rhithral regions. Kownacki (1982) found it to be most abundant in Poland at a station on stony bottoms in an upper-elevation Carpathian pastureland stream, while in the high Tatras it was most often encountered in rapid current in the montane forest zone (700–1500 m elevation), being the dominant species there (Kownacki 1971, Kownacki and Kownacka 1971). Kownacka and Kownacki (1972) clarified the dominant status to those stations with a granite substratum below 1550 m elevation. In the medium to large stony streams of the Little Caucasus Mountains of Georgia (Adzhar) and the Caucasus Mountains of Azerbaijan, this species was among the dominant chironomids (Kowanacki and Zosidze 1980, Kownacki 1985). In Rybi Potok, a polluted stream in Poland, Kownacki (1989) found that *O. rivicola* increased in abundance as organic enrichment decreased. In Germany, Kownacki and Margreiter-Kownacka (1993) collected it in the Alz River at all stations including the soft-bottomed, slower-flowing section immediately below a lake outflow; Reiss and Kohmann (1982) collected it from the banks of the lower Inn River, a large, regulated, primary tributary of the Danube. Fahy (1975) found highest numbers in low to intermediate flows in a low-nutrient, stony stream in Ireland. This is one of the more abundant orthoclads in the Colorado River as well as the upper Arkansas River in Colorado (Herrmann et al. unpublished), and the upper Canadian, Rio Grande, San Juan, and Gila drainages in New Mexico; it occurs on a variety of substrata ranging from boulder-gravel to sand-silt (Sublette unpublished). Ruse et al. (unpublished data) collected adults in the upper Arkansas River at elevations ranging from 1431 to 3042 m.

DISTRIBUTION.—Holarctic; widely distributed throughout much of North America from the high arctic to the lower temperate zones.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 4 ♂♂, 2 ♀P, 1 Pex, river mi 0.0, 947 m elev; 1 ♂, river mi 2.0, 945 m elev; 3 ♂ Pex, river mi 3.4, 941 m elev; 1 ♂, river mi 20.4, 911 m elev; 1 ♂, river mi 31.0, 876 m elev; river mi 31.5, 876 m elev; 1 ♂, river mi 43.2, 861 m elev; 2 ♂♂, river mi 52.7, 846 m elev; 2 ♂♂, river mi 53.0, 846 m elev; 1 ♂, river mi 56.0, 838 m elev; 2 ♂♂, river mi 61.0, 826 m elev; 2 ♂♂, river mi 63.7, 823 m elev; 2 ♂♂, river mi 65.3, 815 m elev; 1 ♂, river mi 88.0, 739 m elev; 1 ♂, river mi 89.0, 736 m elev; 2 ♂♂, river mi 108.0, 699 m elev; 1 ♂, river mi 124.0, 625 m elev.

Orthocladius (Orthocladius) frigidus (Zetterstedt)

Chironomus frigidus Zetterstedt 1838:812; type locality, Greenland.

Orthocladius (Orthocladius) frigidus (Zetterstedt); Soponis 1987:123, subgeneric position, review, synonymy; 1990:53, morphology; Oliver et al. 1990:32, in catalog.

DIAGNOSIS AND DISCUSSION.—Soponis (1987) has characterized all life history stages. The male genitalia are similar to those of some members of the subgenus *Euorthocladius* (Soponis 1990) in which *O. frigidus* was, until recently, included. However, the anal point is usually distinctly broader and the dorsal extension of the eye is longer than in members of that subgenus (Soponis 1990: Fig. 12).

ECOLOGY.—*Orthocladius frigidus* inhabits cool to cold streams, constructing detritus-encrusted silken tubes in moss or algae. It has been reported on stones but seldom on moss and algae in a small stream in central Germany (Ringe 1974), on aquatic mosses (Nolte 1991), from "springs, streams and rivers" (Aagaard et al. 1987), and in an islandic lake, primarily in the littoral splash zone but occasionally as deep as 30 m (Lindegaard 1980). Armitage and Blackburn (1985) found *O. frigidus* in streams with moderate levels of zinc, but it is considered pollution intolerant in the classification of Wilson and McGill (1982). Serra-Tosio (1977) took it from a stream with considerable anthropogenic enrichment, while Cobo and Gonzáles (1991) reported it from 1 of 5 stations receiving organic enrichment on the River Sar in Spain. In a Pyrenean torrent, d'Estaragne, Laville and Lavandier (1977) found this species in small numbers above 2150 m elevation, occurring on boulder-gravel substrata or on moss. In the Ossau Valley in the French Pyrenees, this species had the highest frequency of occurrence, occupying streams at elevations of 500–2000 m; water temperatures ranged from 9° to 16°C (Laville and Vinçon 1991). Schmid (1992) observed this species at significantly higher densities in the main current channel than in the marginal area of a gravel stream, the Oberer Seebach, in Austria; he further reported a tendency towards bivoltinism. Ringe (1974) illustrated 2 major peaks of adult emergence from a small stream in central Germany, 1 in May and the other in November. Fahy (1975) collected this species most often in intermediate flows in a stony, low-nutrient stream system in Ireland. In the high Tatras of Poland it occupied stony bottoms in rapid current (Kownacki 1971, Kownacki and Kownacka 1971); in the Little Caucasus Mountains of Georgia (Adzhar) and in the high Caucasus Mountains of Azerbaijan it was taken from several stations in medium to large, stony-bottomed streams (Kownacki and Zosidze 1980, Kownacki 1985). In Germany, Kownacki and Margreiter-Kownacka (1993) found this species in the Alz River most often some distance below a lake outflow; Lehmann (1971) reported it from the Fulda in areas with strong currents; and Reiss and Kohmann (1982) collected it from the banks of the lower Inn River, a regulated, primary tributary of the Danube. In Lebanon, Moubayed and Laville (1983) reported *O. frigidus* from several stream systems with variable current and substrata, but usually at stations with mosses or macrophytes. It has been taken at elevations from 1746 to 3042 m on gravel/cobble substrates in the Arkansas River of Colorado (Ruse et al. unpublished data). The rarity of *O. frigidus* in the Colorado River is possibly due to the almost constant scouring action of the river in the canyon, which disturbs the preferred gravel and removes algal clumps.

DISTRIBUTION.—Holarctic; in North America this species occurs from California to New Mexico and Colorado, Pennsylvania, and Greenland.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 L, river mi 0.0.

Orthocladius (Orthocladius) mallochi Kieffer

Orthocladius lacteipennis Malloch 1915:524, male; type locality, South Haven, MI.

Orthocladius mallochi Kieffer 1919:191, *nomen novum* for *Orthocladius lacteipennis* Malloch 1915, *non* Lundström 1910.

Orthocladius (Orthocladius) mallochi Kieffer; Soponis 1977:63, revision, adults, immatures, distribution; Savage and Soponis 1983:302, adult morphology; Hudson et al. 1990:11, in list, distribution; Oliver et al. 1990:32, in catalog, distribution.

DIAGNOSIS AND DISCUSSION.—Adults and immatures have been keyed by Soponis (1977).

ECOLOGY.—*Orthocladius mallochi* was one of the rarest Orthocladiinae in a brown-water stream in Alberta, with only 0.03 of 1.0% males/m^2/yr collected (Boerger 1981). It is common in the upper Arkansas River of Colorado where it occurs at elevations of 1431–2905 m (Ruse et al. unpublished data). It occurs in most stream systems in New Mexico (Sublette unpublished).

DISTRIBUTION.—This species has an unusual distribution, with specimens taken from Alberta south to California and New Mexico in western North America and from Northwest Territories south to Illinois and South Carolina in the East.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 204.0.

Paracladius conversus (Walker)

Chironomus conversus Walker 1856:175; type locality, British Isles.

Paracladius conversus (Walker); Hirvenoja 1973:94, revision, adults and immatures; Sublette and Sublette 1979:

80, distribution; Oliver et al. 1990:33, in catalog, distribution.

Diagnosis.—The adults and pupae of the 3 known species have been separated in key by Hirvenoja (1973). Reared material from New Mexico agrees well with Hirvenoja's descriptions as does the single male taken in Grand Canyon.

Ecology.—*Paracladius conversus* is most frequently collected from lakes but is also known from slow-moving streams (Hirvenoja 1973). In Germany, Reiss and Kohmann (1982) collected it from stream margins of the lower Inn River, a large, regulated, primary tributary of the Danube; in the Fulda, Lehmann (1971) reported it from the Potamal region ("Barbenregion"). In the Nida River in Poland, Kownacki (1989) found this species to be generally distributed but occurring in greater abundance in the recovery zone below a sewer outfall. It is known from a zinc-contaminated stream where it constituted <0.5% of the sample (Wilson 1988). It has been statistically associated with *Myriophyllum* in the River Pang in England (Ruse 1992). In the Ossau Valley of the French Pyrenees this was a rare species, occurring in medium to slow streams at 800–850 m elevation; maximum water temperatures were 16° to 18°C (Laville and Vinçon 1991). In small, interrupted stream systems of Lebanon this species was found at 3 stations with macrophytes (Moubayed and Laville 1983). In New Mexico it was often taken near stream margins (Sublette and Sublette unpublished data).

Distribution.—Arizona to New Mexico and Colorado; Pennsylvania. It is possible that some records of *P. alpicola* (Zetterstedt) from the Nearctic region are actually this species.

Material examined.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 2 ♂♂, river mi 246L, 365 m elev, 13-XI-1975.

Parakiefferiella subaterrima
(Malloch)

(Figs. 40–43)

Camptocladius subaterrimus Malloch 1915:512, male; type locality, bank of Mississippi River, Grand Tower, IL (INHS).

Parakiefferiella torulata Sæther 1969:138, male with associated pupal and larval exuviae; type locality, Whiteshell Park, Manitoba, ditch.

Maricladius subaterrimus (Malloch); Sublette 1970:85, generic position, review.

Parakiefferiella subaterrima (Malloch); Cranston and Oliver 1988:443, generic position, review, synonymy, distribution.

Parakiefferiella subaterrima (Malloch); Oliver et al. 1990:33, in catalog, distribution.

Diagnosis and discussion.—The male can be recognized by the presence of a distinct R_{2+3} which becomes evanescent apically, an antennal ratio usually about 1.0 (0.68–1.34), and, above all, the male genitalia. The genitalia (Fig. 40) have typically a bluntly acute anal point; compression due to more or less flattening by the cover glass results in considerable variation in appearance of the anal point as well as the basidorsal and basiventral gonocoxite lobes. Proximally, the basidorsal gonocoxite lobe usually has visible a transverse apodeme that appears as a darkened bar. Northern specimens have a higher number of anal point setae and higher antennal ratio (based on Sæther 1969).

The pupa, based on extensive rearings from New Mexico, differs in some features from that described by Sæther (1969): the frontal apotome has small frontal setae (Fig. 41), there is a small egg-shaped thoracic horn with fine apical denticles present (Fig. 42), pedes spurii B are present on T II and III, and the shagreen pattern on the abdomen is much weaker (Fig. 43). Specimens from the Chama River in New Mexico near the Colorado state line have heavier shagreen than those taken from the Rio Grande in Doña Ana County in New Mexico near the Texas state line. Thus, the pupa described from Manitoba (Sæther 1969) with the terga almost completely covered by shagreen may represent the extreme of a north–south cline.

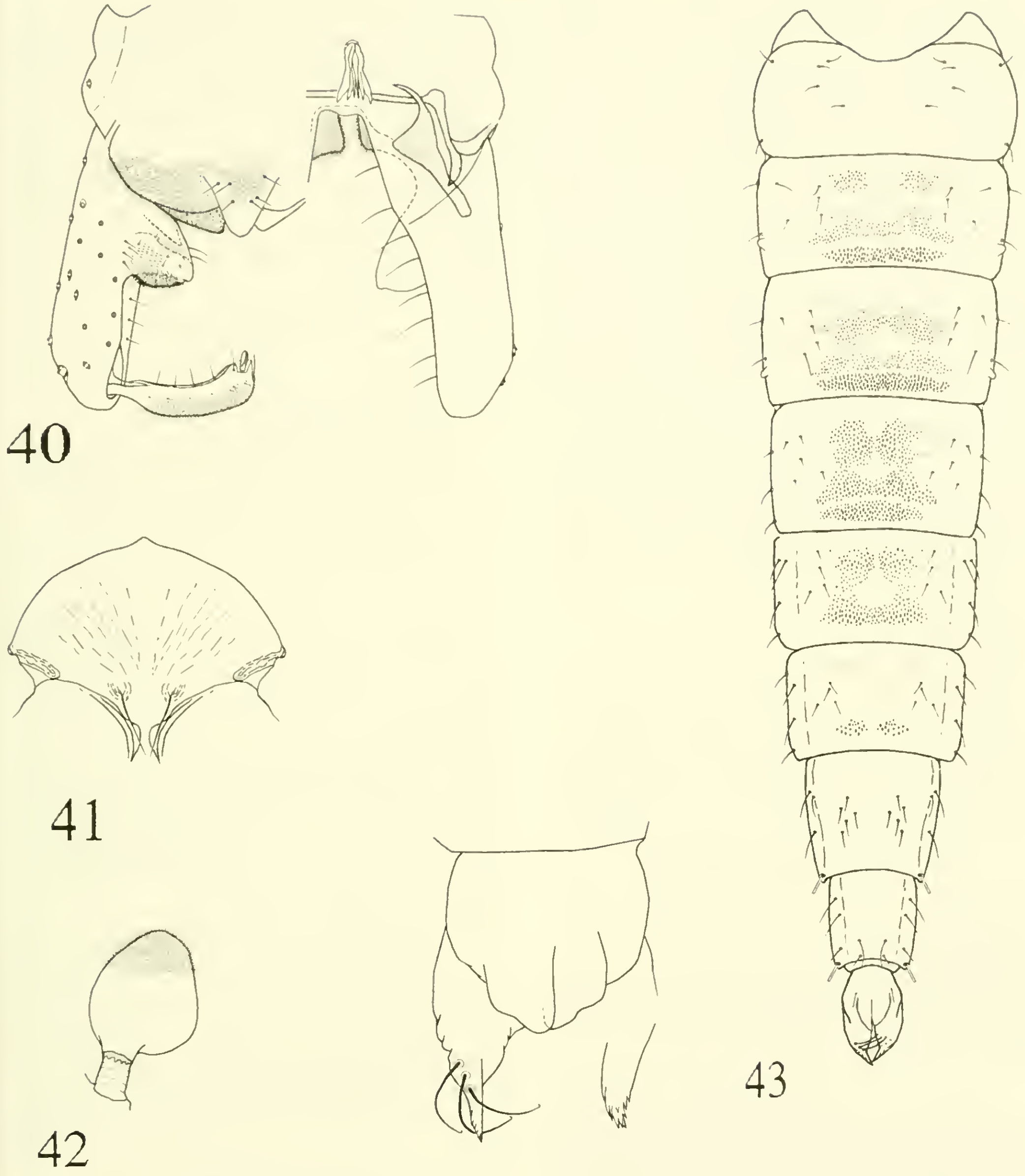
Ecology.—This is a common inhabitant of the upper Arkansas River in Colorado, found at elevations ranging from 1444 to 2771 m (Ruse et al. unpublished data).

Distribution.—Northwest Territory east to Quebec and south to California and Illinois.

Material examined.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 89.0, 732 m elev, 8-I-91. Other material examined: California, Colorado, New Mexico, and Utah.

Parametriocnemus lundbeckii
(Johannsen)

Metriocnemus lundbeckii Johannsen 1905:302, *nomen novum* for *Chironomus nanus* Lundbeck 1898:285, *non* Meigen 1818; type locality, Greenland: Oliver et al. 1990:34, in catalog, distribution; Epler 1995:6.65, larva, distribution.



Figs. 40–43. *Parakiefferiella subaterrima*. Male: 40, genitalia. Pupa: 41, frontal apotome; 42, thoracic horn; 43, abdominal chaetotaxy and shagreen, including details of anal lobe and apex of anal lobe.

Parametriocnemus lundbecki (Johannsen); Sublette 1967:537, review; Sæther 1969:115, review, synonymy, distribution; Simpson and Bode 1980:56, larva, ecology; Cranston et al. 1983:261, larva; Simpson 1983:320, ecology; Coffman et al. 1986:265, pupa; Cranston et al. 1989: 310, male; Hudson et al. 1990:11, in list, distribution.

DIAGNOSIS AND DISCUSSION.—The adults and pupae have been well characterized by Sæther (1969).

ECOLOGY.—The North Carolina biotic index (NCBI) value for *Parametriocnemus lundbeckii* is 3.7 (Lenat 1993), which agrees with the Simpson and Bode (1980) observation that the species is restricted to relatively clean water. It has been listed by Singh and Harrison (1984) as having 3 periods of adult emergence, but the species was not commonly taken, comprising only 1.84% of all chironomids collected; this was similar to Boerger's (1981) findings, which listed only 0.5 of 1.0% males/m^2/yr of the total Orthocladiinae. The cohort growth is asynchronous with maximal growth in the spring (Berg and Hellenthal 1992a). Beckett (1992) collected the species in a large temperate river on artificial plate samplers in low numbers during most months except June–August. *P. lundbeckii* was more frequently taken from an acid, poorly buffered Precambrian Shield stream with a boulder-cobble bottom covered with thick growths of *Fontinalis* (Rempel and Harrison 1987). McShaffrey and Olive (1985) found only diatoms in the gut contents of larvae. In the upper Arkansas River of Colorado this is an uncommon, but rather widely distributed, species occurring at elevations ranging from 1444 to 3042 m (Ruse et al. unpublished data). In New Mexico *P. lundbeckii* is widely distributed in northern and western cool- to coldwater streams (Sublette and Sublette 1979). Epler (1995) reported the larvae as being sensitive to organic pollution.

DISTRIBUTION.—Alberta east to Quebec and Greenland, south to California and Florida.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 133.5, 625 m elev, 17-VIII-75.

Paraphaenocladius exagitans (Johannsen)

Metriocnemus exagitans Johannsen 1905:303; type locality, New York.

Paraphaenocladius exagitans (Johannsen); Sublette 1967:543, review, generic position; Hudson et al. 1990:12, in list, distribution; Oliver et al. 1990:34, catalog, distribution, synonymy.

DIAGNOSIS AND DISCUSSION.—The hairy wings, retracted R_{4+5} ending proximal to the apex of M_{3+4}, and features of the male genitalia (Sublette 1967: Figs. 36, 37) differentiate this species from other Nearctic congeners.

ECOLOGY.—Members of this genus in the Palearctic region are reported to be terrestrial, living in damp soil adjacent to water bodies (Strenzke 1950). In the Nearctic, however, "at least semiaquatic and perhaps truly aquatic species occur in streams and springs" (Cranston et al. 1983). Rosenberg et al. (1988) reported *Paraphaenocladius exagitans* emerging from a fen in western Ontario, indicating at least a semiaquatic existence for this species. Ruse et al. (unpublished data) collected this species only once along the Arkansas River in Colorado at an elevation of 2338 m; adults probably came from nearby spring seeps or marshy areas.

DISTRIBUTION.—South Dakota east to New York, south to Arizona and New Mexico.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 31.8, 876 m elev; 1 ♂, river mi 124.0, 625 m elev.

Pseudosmittia nanseni (Kieffer)

Psectrocladius nanseni Kieffer 1926:82; type locality, Ellesmere Island, Northwest Territories.

Prosmittia nanseni (Kieffer); Oliver 1963:177, generic position, in list; Sæther et al. 1984:270, review of holotype.

Pseudosmittia nanseni (Kieffer); Cranston and Oliver 1988:451, generic position, added description of male, distribution; Hudson et al. 1990:13, in list, distribution.

Pseudosmittia n. sp.1; Sublette and Sublette 1979:83, misidentification, distribution.

DIAGNOSIS.—The male genitalia (Sæther et al. 1984: Fig. 12; Cranston and Oliver 1988: Fig. 20) are distinctive. Immature stages are unknown.

DISCUSSION.—This wide-ranging species shows considerable variation between northern and more southern populations (Cranston and Oliver 1988). Dr. O.A. Sæther, University of Bergen, suggests the nominal species is actually a complex of related forms (personal communication).

ECOLOGY.—*Pseudosmittia nanseni* is probably a madicolous species, as Wrubleski and Rosenberg (1990) reported low numbers of it from emergent vegetation where apparently the aquatic-terrestrial interface provides a habitat. Presumably, wet algal strands in the splash zone on the rock faces of the canyon wall in Grand Canyon are similar to the interface found on emergent aquatic vegetation.

DISTRIBUTION.—Alaska to Greenland, south to California, east to Georgia.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 6.0, 945 m elev.

Tvetenia vitracies (Sæther)

Eukiefferiella vitracies Sæther 1969:49, male, female, and pupa.

Tvetenia vitracies (Sæther); Sæther and Halvorsen 1981:271, generic position; Coffman et al. 1986:293, pupa.

Tvetenia calvescens (Edwards); Sublette and Sublette 1979:74, review, distribution, misidentification.

DIAGNOSIS AND DISCUSSION.—The genitalia are very similar to those of *Tvetenia calvescens* (Edwards), *T. discoloripes* (Goetghebuer), and *T. bavarica* (Goetghebuer) (cf. Pinder 1978: Figs. 105 b, c; Lehmann 1972: Figs. 65, 70, 71, 77); however, the antennal ratios of *T. calvescens* (Edwards) and *T. bavarica* (Goetghebuer) are much lower (0.6–0.8 vs. 1.03–1.35). The pupal thoracic horn and abdominal chaetotaxy of *T. vitracies* have been briefly described by Sæther (1969) and figured by Coffmann et al. (1986: Fig. 9.75). It is very similar to that of *T. verralli* (Edwards) (Langton 1991), but the pupa of that species lacks the fine-pointed spines at the apex of the anal lobe. The adult male of *T. verralli* has much stronger crista dorsalis on the gonostylus (cf. Pinder 1978: Fig. 105A).

ECOLOGY.—Larvae of the *discoloripes*-group are most frequently found in larger, warmer rivers, most often in association with *Cladophora* (Bode 1983). Ruse et al. (unpublished data) collected *T. vitracies* in the upper Arkansas River of Colorado at elevations ranging from 1497 to 1879 m.

DISTRIBUTION.—Arizona, California, Colorado, New Mexico, Ontario, and Saskatchewan. Possibly, some of the North American records of *T. calvescens* are actually this species since the male genitalia appear to be virtually indistinguishable.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 5 ♂♂, river mi 31.5, 876 m elev; 6 ♂♂, river mi 31.8, 876 m elev; 1 ♂, river mi 43.0, 861 m elev; 3 ♂♂, river mi 94.9, 715 m elev; 2 ♂♂, river mi 61.0, 826 m elev; 1 ♂, river mi 123.0, 632 m elev; 1 ♂, river mi 135.0, 594 m elev; 2 ♂♂, river mi 186.0, 491 m elev; 1 ♂, river mi 204.0, 454 m elev; 1 ♂, river mi 225.0, 411 m elev.

SUBFAMILY CHIRONOMINAE

Tribe Chironomini

Apedilum subcinctum Townes

Apedilum subcinctum Townes 1945:33; type locality, Reno, NV; Epler 1988:112, review, generic reassignment; 1995:7.24, larva, distribution; Hudson et al. 1990:26, in list, distribution.

Paralauterborniella subcincta (Townes); Pinder and Reiss 1986:418, pupa.

Paralauterborniella subcincta subcincta (Townes); Bath and Anderson 1969:172, larva.

DIAGNOSIS AND DISCUSSION.—The male is recognized most readily by the features of genitalia (cf. Townes 1945: Fig.24; Epler 1988: Fig. 1e–k). The pupa has been characterized by Pinder and Reiss (1986) and Epler (1988).

ECOLOGY.—*Apedilum subcinctum* lives in aquatic vegetation, including mat algae. It sometimes becomes a pest in concrete-lined irrigation canals.

DISTRIBUTION.—California to Ontario, south to Jalisco.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 61.0, 826 m elev; also, material from California, Colorado, New Mexico.

Chironomus decorus
Johannsen

Chironomus decorus Johannsen 1905:239; type locality, Ithaca, NY; adults and immature stages.

Chironomus decorus Johannsen; Sublette and Sublette 1979:86, review, distribution; Martin et al. 1979:131, karyotype.

DIAGNOSIS AND DISCUSSION.—The male genitalia (Townes 1945: Fig. 136a), together with abdominal coloration consisting of saddle-shaped darker markings on terga II–V (heaviest on II–IV, occasionally evanescent on V) and a foretarsus without a beard, will differentiate the species. However, there are at least 10 Nearctic species in this complex (Martin et al. 1979), and identifications are somewhat uncertain at this time. One of the authors (JES) has examined the holotype at Cornell University, and the Grand Canyon material cannot be separated from it on adult morphology. The larva and pupa cannot be adequately separated. The most reliable separation remains through karyological examination.

ECOLOGY.—*Chironomus decorus* is primarily lentic but occurs widely in stream systems in backwater pools and river stretches with little current. As do other members of the genus, this species lives on soft, muddy substrata, occasionally on sandy-silt. In New Mexico it occurs in every major stream system in the state (Sublette and Sublette 1979).

DISTRIBUTION.—Throughout much of North America; however, many of the literature records of this and its junior synonym, *Chironomus attenuatus* Walker, are suspect. Karyological or DNA studies are needed to define the many populations.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 259.0R, 8-V-90; 1 ♂, river mi 268.5, 21-VII-75, LES.

Chironomus (Chironomus) decorus Johannsen complex

At least 2 additional species of this group occur in Grand Canyon, based on males with adequate genitalia visible in limited slide-mounted material. However, this material was not considered sufficient upon which to base new species descriptions. With additional material in hand a better appraisal will be possible. The localities for these are described below

Chironomus n. sp. 1

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 2 ♂, river mi 246.0L, 13-XI-75; ? 1 ♀, Pex, river mi 209.0L, 4-XII-91.

Chironomus n. sp. 2

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 269.5, 21-VII-75.

Chironomus (Chironomus) utahensis Malloch

Chironomus utahensis Malloch 1915:438; type locality, Kaysville, UT; Schaller and English 1976:300, cytology; Sublette and Sublette 1979:89, distribution; Martin et al. 1979:139, karyotype.

Tendipes (Tendipes) utahensis (Malloch); Townes 1945: 127, review.

Chironomus (Chironomus) utahensis Malloch; Oliver et al. 1990:43, distribution; Wülker et al. 1991:71, review, immatures and adults, karyosystematic position.

DIAGNOSIS AND DISCUSSION.—The distinctive male genitalia will serve to differentiate this species from other Nearctic species (cf. Townes 1945: Fig. 143). Immatures have been characterized by Wülker et al. (1991).

ECOLOGY.—*Chironomus utahensis* is primarily lentic, inhabiting water bodies ranging from large lakes and reservoirs to shallow ponds in Manitoba and playa lakes on the Llano Estacado of New Mexico. This species is an uncommon inhabitant of pool environments with silty sand substrata; it also may occur in backwaters. Similar collections of the lentic *C. decorus* complex have been taken in the Arkansas River in Colorado and Pecos River and Rio Grande in New Mexico (Sublette unpublished data).

DISTRIBUTION.—This widely distributed western species ranges from Alberta and Manitoba south to California and New Mexico.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, 1 ♂ Pex, 1 Lex, river mi 53.0, 847 m elev; ? 1 ♀, river mi 0.0R, 11-VII-90, J.S.; ? 1 ♂, L, Pex, river mi 31.0R, 1-II-90, J.S.

Cyphomella gibbera Sæther

Cyphomella gibbera Sæther 1977:103; type locality, Yankton, SD, male, pupa; Pinder and Reiss 1986:379, pupa; Oliver et al. 1990:45, distribution.

DIAGNOSIS AND DISCUSSION.—The male is very near *Cyphomella cornea* Sæther in genitalic features but differs in having 8–11 setae on the inferior volsella while *C. cornea* has 0–1; the superior volsella lacks setae while in *C. cornea* there are usually 4 (cf. Sæther 1977: Figs. 37D, F). Immature stages have been figured by Sæther (1977: pupa, Fig. 37A, B; larva, Fig. 38; Pinder and Reiss 1983: larva, Fig. 10.13) as *Cyphomella* sp.

ECOLOGY.—Ruse et al. (unpublished data) collected this species in the upper Arkansas River of Colorado at an elevation of 1497 m. In New Mexico this species occurs in a wide variety of habitats ranging from cold- to warm-water streams with substrata ranging from gravel to sand-silt (Sublette and Sublette 1979).

DISTRIBUTION.—Saskatchewan and South Dakota south to Arizona and New Mexico.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 2 LL, river mi 61.0, 826 m elev; 1 L, river mi 87.5, 740 m elev; 1 L, river mi 187.5, 488 m elev, 19-IX-91, M.S.

Phaenopsectra profusa (Townes)

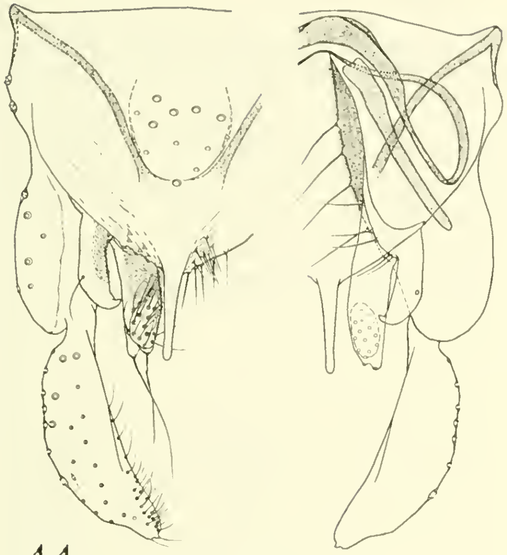
(Figs. 44–48)

Tanytarsus (Tanytarsus) profusus Townes 1945:73; type locality, Reno, NV, male.

Phaenopsectra profusa (Townes); Grodhaus 1987:137, generic position, morphology, ecology; Oliver et al. 1990:51, distribution.

Phaenopsectra n. sp. 1; Sublette and Sublette 1979:103, distribution, misidentification; Martin et al. 1979:151, karyotype.

The male has been briefly described by Townes (1945). The following is given to supplement his description.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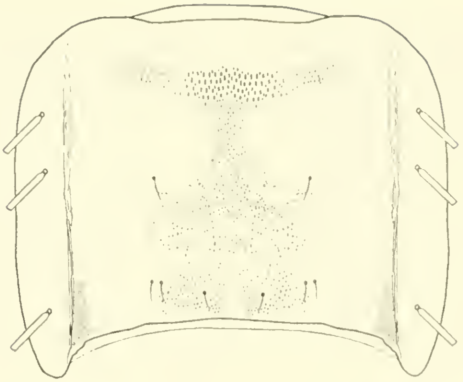
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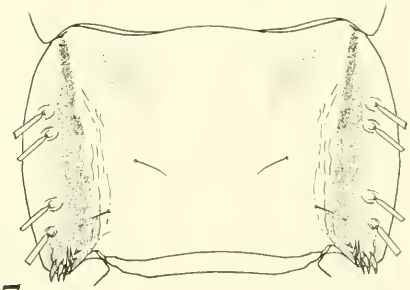
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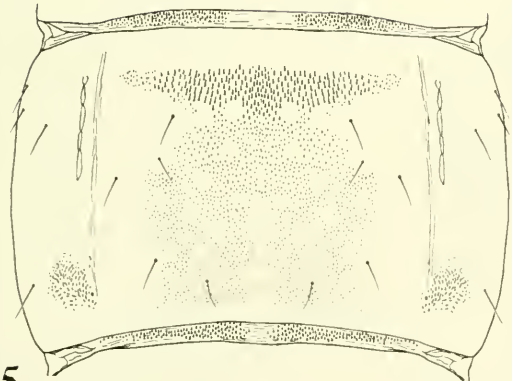
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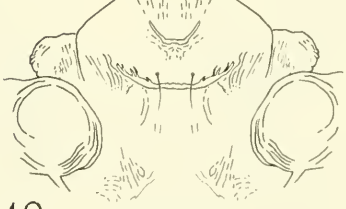
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Figs. 44–48. *Phaenopsectra profusa*. Male: 44, genitalia. Pupa: 45, tergum IV; 46, tergum VI; 47, tergum VIII. *Polypedilum (Polypedilum) obelos*. Pupa: 48, frontal apotome.

MALE.—*Coloration*: Head, thorax, and abdomen largely blackish brown; scutellum somewhat paler brown; legs with coxae dark, remainder mostly stramineous except knees, which are slightly darker; haltere knob pale; abdomen largely dark with the posterolateral margins of the terga paler brown; genitalia infuscate.

Head: Antenna with 13 flagellomeres. Antennal ratio 1.9–1.96. Palpal proportions 70:164: 179:289 µm. Eyes with dorsal extension long and parallel-sided. Ocular ratio 0.19. Clypeus quadrangular, slightly longer than wide, with 21–23 setae; clyp/ped ratio 0.76. Temporal setae 14, in a single row, reaching about halfway from the dorsal apex of the eyes to the midline of the head.

Thorax: Antepronotum greatly narrowed near the dorsal apex and closely appressed to the mesonotal continuation (cf. Townes 1945: Fig. 230). Thoracic chaetotaxy: lateral antepronotals lacking; dorsocentrals 16–18, in a partial double row; acrostichials 15–16, mostly in 2 rows; prealars 7; supra-alars lacking; scutellars 24–32, in a strewn pattern.

Wing: Membrane with heavy macrotrichia distal to the apex of R_1 and with sparse macrotrichia extending almost to the wing base. Costa not extended beyond R_{4+5}, which ends considerably distal to M_{3+4} at 0.93 of the distance between apex of M_{3+4} and M_{1+2}. R_{2+3} closely parallels R_1, ending at about 0.2 of the distance between apex of R_1 and R_{4+5}. Venarum ratio 1.0–1.04. Wing length 2.75–2.79 mm. Squama with 15–18 marginal setae. Wing vein setae: R 27, R_1 35, R_{4+5} 63, M_{1+2} 48, M_{3+4} 21, Cu_1 19, An 25.

Legs: Foretibial scale with a minute spine, very similar to that illustrated by Townes (1945: Fig. 249); middle tibial combs with a single spur; hind tibial combs with 2 spurs, of which 1 is slightly shorter than the other. Pulvilli conspicuous, almost as long as the claws. Leg ratios: P I 1.10–1.15; P II 0.57; P III 0.73.

Abdomen: Abdominal tergal setae scattered, becoming denser at the lateral margins.

Genitalia (Fig. 44): Ninth tergum with 12–16 setae. Gc/Gs ratio 0.95.

PUPA.—*Cephalothorax*: Cephalothorax brown; wing sheaths mostly pale but outlined with brownish margins. Frontal setae present on the frontal tubercles very similar to that illustrated for *P. flavipes* (Meigen) (cf.Pinder and Reiss 1986: Fig. 10.59A); frontal setal length 58 µm. Thoracic horn base also similar to that of *P. flavipes* (cf. Pinder and Reiss 1986: Fig. 10.59C). Median suture with strong tubercles on either side near the anterior end and with a smaller patch near the posterior end on either side. Precorneal setae very weak, with 1 longer and 2 slightly shorter setae. Posterior dorsocentrals small, in a line below the posterior tubercle patch; anterior dorsocentrals not discernible. Wing sheaths without bacatiform papillae or nasiform tubercles.

Abdomen: Abdomen mostly pale but with blackish spots at the corners of conjunctiva I–II, II–III, III–IV, and IV–V; lateral margins of terga V–VIII with a narrow brown band that becomes progressively broader posteriorly. Abdomen length 4.85–5.00 mm. Shagreen pattern and chaetotaxy very similar to *P. flavipes* (cf. Pinder and Reiss 1986: Fig. 10.59D), but with the anterior band of shagreen not conspicuously heavier than the posterior; tergum IV (Fig. 45), tergum VI (Fig. 46), and tergum VIII (Fig. 47). Pedes spurii B on terga I and II. Tergum II hooks 69–72 in a single row. Anal lobe with 27–42 swim fringe setae.

DIAGNOSIS AND DISCUSSION.—The male of this species is only weakly separated, based on color features, from the closely related *P. obediens* (Johannsen) (Townes 1945). These 2 species may prove ultimately to be conspecific when more material is available for examination. The pupa is very similar to *P. flavipes* but differs in having a more heavily tuberculate cephalothorax.

ECOLOGY.—Grodhaus (1987) took *Phaenopsectra profusa* from temporary pools in California and suggested that the species maintains itself in permanent waters and opportunistically invades temporary pools, since it also has been found in rice fields, reservoirs, and sewage lagoons. Ruse et al. (unpublished data) collected adults of this species in the upper Arkansas River of Colorado at elevations ranging from 1431 to 2944 m. Its rarity in the Colorado River in Grand Canyon bespeaks a paucity of lentic habitats, principally small backwater and side pools.

DISTRIBUTION.—Washington to Montana south to California and New Mexico.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 Lex, Pex, ♂, river mi 31.8, 876 m elev; 1 P♂, 3 LL, river mi 53.0, 847 m elev; 2 LL, river mi 225.0, 411 m elev.

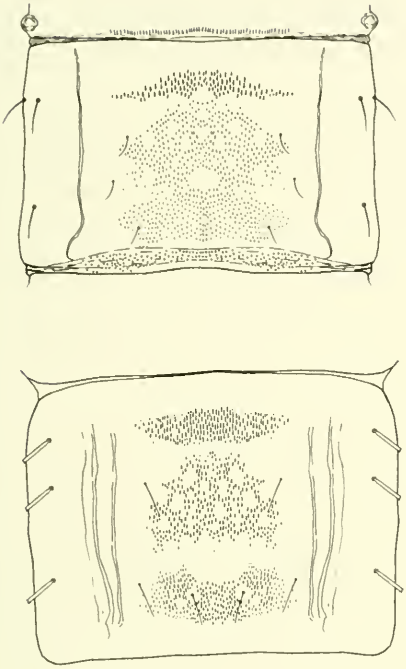
Polypedilum (Tripodura) obelos
Sublette & Sasa

(Figs. 49–52)

Polypedilum (Tribelos) obelos Sublette & Sasa 1994:50; type locality, Lavaderos, Guatemala, male and female.

PUPA.—Total length 4.67, 5.52 mm (2).

Cephalothorax: Frontal apotome without tubercles (Fig. 48); frontal setal length 62 µm. Thoracic horn with 3 posterior branches and about 5 anterior branches, similar to that of



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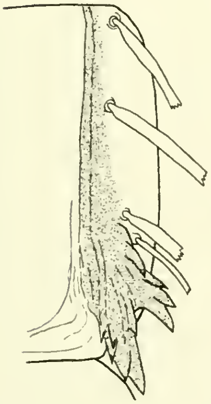

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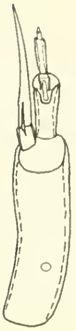

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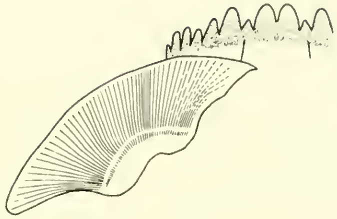

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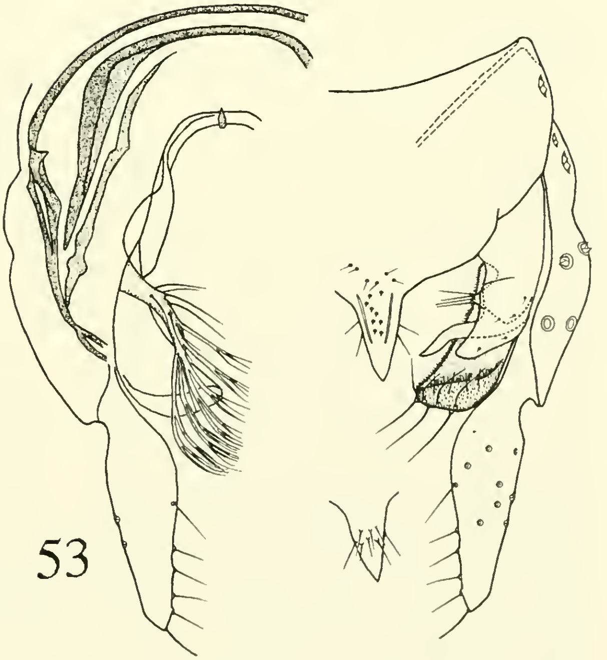

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Figs. 49–53. *Polypedilum (Polypedilum) obelos.* Pupa: 49, terga III (above) and VI (below) shagreen and chaetotaxy; 50, posterolateral spur of tergum VIII. Larva: 51, antenna; 52, mentum and ventromental plate. *Cladotanytarsus (Cladotanytarsus) marki.* Male: 53, genitalia.

Polypedilum (Tripodura) epomis Sublette and Sasa (Sublette and Sasa 1994: Fig. 170). Precorneal setae 2, 52 µm in length, subequal. Median suture with moderate tubercles anteriorly on either side; posteriorly becoming weakly rugose. Dorsocentral setae minute, anteriorly with DcS_1 and DcS_2 contiguous and posteriorly with DcS_3 and DcS_4 the same. Bacatiform papillae and nasiform tubercles lacking.

Abdomen: Abdomen length 3.48, 4.15 mm (2). Tergum I with weak reticulation; PSB I and II present. T II apical hooks 54, 62 (2). PSA present on S IV–VI. Terga III–V shagreen as in Figure 49; T VI with weaker shagreen so that the anterior, medial, and posterior transverse bands are separate. Intersegmental membrane III/IV and IV/V with weak shagreen (Fig. 49). Lateral abdominal setae: II–IV with 3 filiform setae, V–VI with 3 lamellate setae, and VII–VIII with 4. Posterolateral spur of T VIII (Fig. 50). Anal lobe with 38, 42 (2) fringe setae.

LARVA.—Head capsule yellowish except for tips of mandibles, mentum, and occipital ring. Ventral head length 160 µm (1).

Antenna (Fig. 51): Length 90 µm (1); AR 0.80; lauterborn organs large, extending past 3rd segment.

Head and mouthparts (Fig. 52): Mentum with 16 teeth, similar to other members of the genus. Ventromental plate (Fig. 52) with 40–61 fine striae. Premandible with a conspicuous brush, 2 apical teeth, and 1 basal shelf-like tooth. Mandible length 114 µm; seta subdentalis attenuate, down-curved at tip, extending past the basal tooth, similar to that illustrated by Pinder and Reiss (1983: Fig. 10.60C); subapical tooth heavy, scarcely exceeded in length by the apical tooth; mola with 1 very weak denticle; seta interna with numerous fine branches, major branches not discernible. Pecten epipharyngis, chaetulae laterales, ungula, and basal sclerite similar to that of *P. (Tripodura) griseopunctatus* (Malloch) (Soponis and Simpson 1992), but with 5 denticles in each of the lateral plates of the pecten epipharyngis and 6 chatulae laterales on each side; S I and S II simple, fimbriate. Chaetae 5 on each side, weakly fimbriate. Spinulae 2. Lacinial chaetae of maxilla 3, the most anterior one heaviest, reaching to midline of head; 2nd about as long but narrower, and 3rd greatly reduced. Maxillary palpus slightly longer than wide, with at least 7 apical sensillae. Dorsal labral sclerites obscured.

Body: Anterior parapods separate, mostly with pectinate claws. Procerci each with 6 terminal setae and 2 anterior setae; L/W of procercus about 1.0. Claws of anal parapod yellow, simple.

DIAGNOSIS.—This species closely resembles *P. (Tripodura) pterosopilus* Townes in wing features but differs from that species in having the basal dark spot in cell R_5 clearly separated from the r-m crossvein and having spots along the anal margin broader and heavier (cf. Sublette and Sasa 1994: Fig. 181). Male genitalia anal point is longer and more lanceolate (cf. Sublette and Sasa 1994: Fig. 182) than in *P. pterosopilus* (Townes 1945: Fig. 32). The genitalia of *P. (Tripodura) labeculosum* (Mitchell) are more similar to this species (cf. Sublette 1960: Fig. 1C), but the wing spots of *P. labeculosum* are distinctively different (cf. Townes 1945: Fig. 211). Immature stages in this genus are still inadequately known. Of the known southwestern larvae this species most closely resembles *P. labeculosum* in having antennal segments 3–5 about equal to segment 2, ventromental plates finely striate (30–47 striae), head capsule largely pale, and posterior margin of the ventromental plate not strongly sinuate. This species differs, however, in having the 5th antennal segment minute and scarcely distinguishable. The pupa differs from most other southwestern species in having the anterior band of shagreen only slightly greater density than the middle and posterior bands of T II–VI. This, coupled with the heavy, somewhat divided, posterolateral spur of T VIII, presents a unique appearance among the southwestern *Polypedilum*.

DISCUSSION AND ECOLOGY.—The presence of *P. obelos* in Grand Canyon represents the northernmost occurrence of this recently described Neotropical species. The related *P. labeculosum* and *P. pterosopilus* also represent probable Neotropical forms with range extensions into the southwestern United States.

DISTRIBUTION.—Guatemala, Arizona, New Mexico

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂ and Pex, river mi 61.0, 663 m elev; 1 ♂ and Pex, 1 Lex, river mi 166.0, 646 m elev.

Polypedilum (Tripodura) *apicatum* Townes

Polypedilum (Tripodura) apicatum Townes 1945:39; type locality, Las Vegas Hot Springs, NM; Boesel 1985:258, review; Oliver et al. 1990:52, catalog, distribution.

Diagnosis and discussion.—Features of the male genitalia and the characteristic spotted wing are distinctive (cf. Townes 1945: Figs. 31, 207).

Ecology.—This species is found at low elevations in the Southwest and has been collected in desert springs.

Distribution.—California to Colorado and New Mexico; Illinois.

Material examined.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 164.5, 533 m elev; 1 ♂, river mi 166.5, 532 m elev.

Tribe Tanytarsini

Cladotanytarsus marki
Sublette, new species
(Fig. 53)

Holotype male.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, river mi 174.3, 518 m elev, UV trap, LES (CAS).

Coloration: Head, antepronotum, thoracic vittae, preepisternum, a spot on the pleura, and postnotum blackish brown; humeral, prescutellar, and pleural areas and scutellum yellowish; legs and abdomen dark.

Head: Antenna with 13 flagellomeres. Antennal ratio 0.72 (0.60–0.64; 3). Palpal proportions 23:78:78:125 µm. Eyes reniform; ocular ratio 0.71 (0.64–0.72; 3). Clypeus truncate triangular, width at base 0.65 of width of antennal pedicel; with 8 (8–10; 4) setae. Temporal setae 9 (8–9; 4), in a single row, reaching to over halfway to midline of the head.

Thorax: Antepronotum triangular, evanescent dorsally. Thoracic chaetotaxy: lateral antepronotals lacking; dorsocentrals 7 (5–6; 4), in a single row; acrostichials 5 (5–6; 4), partially in 2 rows; prealars 1(1; 4); supra-alars lacking; scutellars 2 (2–4; 3), in a single row.

Wing: Membrane with sparse macrotrichia at the tip; R_{4+5} ends very slightly proximal to apex of M_{1+2}. R_{2+3} ends at 0.65 (0.56–0.65; 4) of the distance between apex of R_1 and R_{4+5}. Venarum ratio 1.25 (1.27–1.31; 5). Wing length 1.26 (1.18–1.45; 4) mm. Wing vein setae: R 10 (7–10; 4), R_{4+5} 4 (1–5; 4), M_{1+2} 15 (7–15; 4).

Legs: Foretibial spine length 12 µm; middle tibial spurs subequal, lengths 10 µm; hind tibial spur lengths 10/8 µm. Pulvilli vestigial. Leg ratios: P I 1.58 (1.89–1.97; 3); P II 0.53 (0.53–0.56; 3); P III 0.65 (0.61–0.67; 3). Sensilla chaetica P II 2 (2; 3).

Abdomen: Genitalia (Fig. 53). Ninth tergum with 6 (3–11; 4) setae; ventral anal point setae extending slightly beyond middle of anal point (Fig. 53, inset). Gc/Gs ratio 1.43 (1.26–1.45; 4).

Diagnosis and discussion.—The medially concave inferior volsella separates this species from all described Nearctic *Cladotanytarsus* except *C. daviesi* Bilyj and *C. pinnaticornis* Bilyj. In those species the anal point spinulae have multiple points at the tip with the spinulae and 9th tergum setae distinctly separated in both size and shape, while *C. marki* has simple tips so that the spinulae grade into the 9th tergum setae.

Paratypes.—AZ: Coconino Co., Colorado River, Grand Canyon National Park, 1 ♂, river mi 108.5, 663 m elev, 26-XI-91, TCM; 4 ♂♂, collected with the holotype ♂ (CAS, USNM).

This species is dedicated to the son of JES, Dr. J. Mark Sublette, who has devoted many hours in the field in pursuit of elusive midges.

Ecology.—This species has been collected in cold-stenothermic conditions in both steep, narrow, bedrock-constrained and wider reaches of the mainstream Colorado River.

Distribution.—This species has been collected only in the lower half of the Colorado River corridor in Grand Canyon, Arizona.

Micropsectra sp.

Diagnosis and discussion.—A single female pupal exuvium was taken at Lees Ferry on 30 December 1990, but the lack of knowledge on female pupal morphology prevented identification to the species level.

Ecology and distribution.—The most common southwestern *Micropsectra* is *M. nigripila* (Johannsen), which has a very broad ecological tolerance, occurring in a variety of flowing water.

Material examined.—AZ: Coconino Co., Grand Canyon National Park, Colorado R, 1 ♀ Pex, river mile 0.0, 950 m elev, 30-XII-90.

Rheotanytarsus hamatus
Sublette and Sasa

Rheotanytarsus hamatus Sublette and Sasa 1994:52; type locality, Rincon, Guatemala.

Diagnosis and discussion.—The genitalia of the males available are in rather poor condition; however, the strongly hooked gonostylus, short medial volsellus, and distinctively shaped superior volsellus are clearly visible (cf.

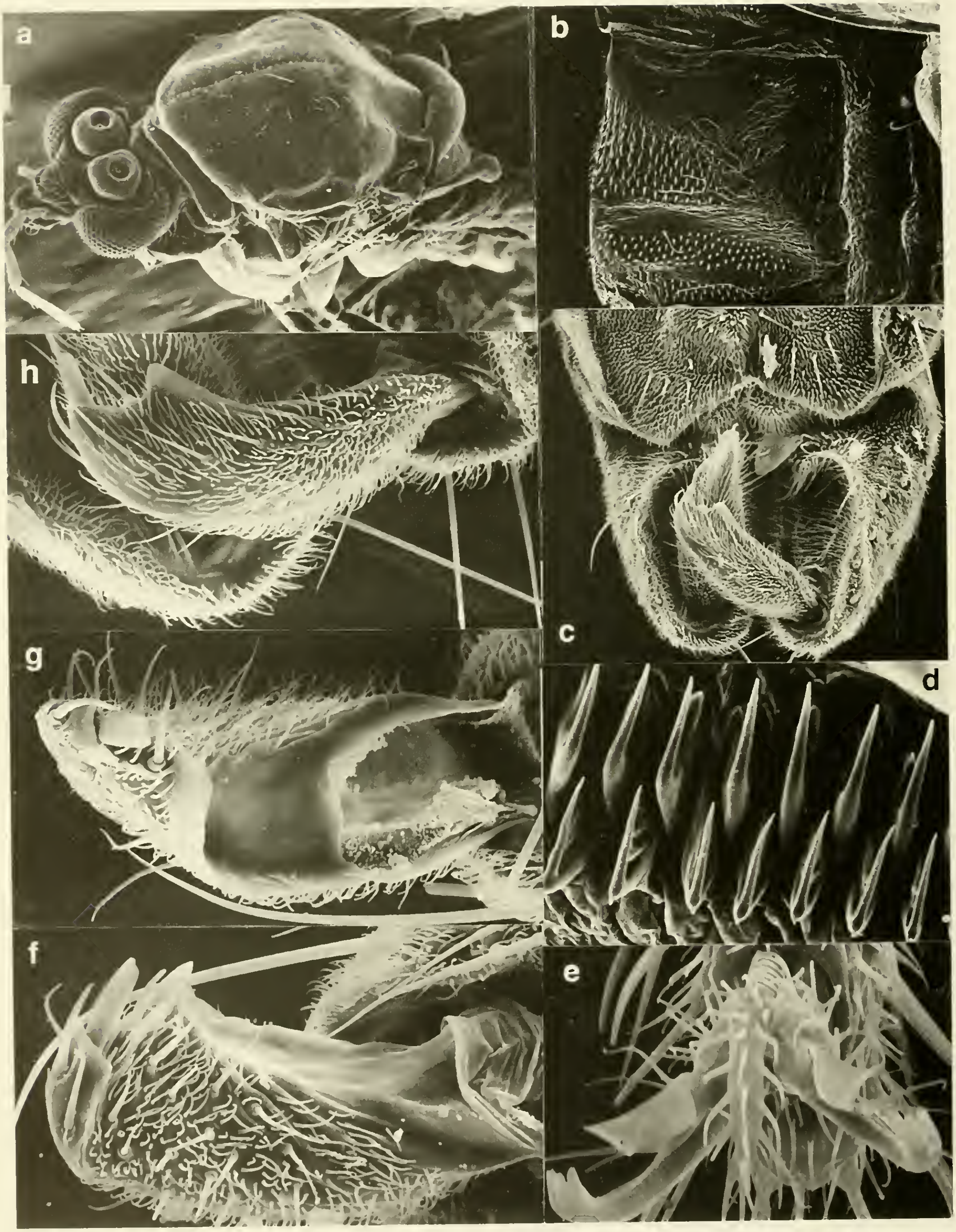

Fig. 54. *Cricotopus (Cricotopus) blinni*, scanning electron micrographs (clockwise from top left): (a) male, head and thorax (dorsolateral view); (b) pupa, tergum III (lateral view); (c) male, genitalia; (d) pupa, recurved hooks of tergum II; (e) male, claws and associated structures; (f) male, gonostylus (ventral); (g) gonostylus (medial); (h) gonostylus (lateral).

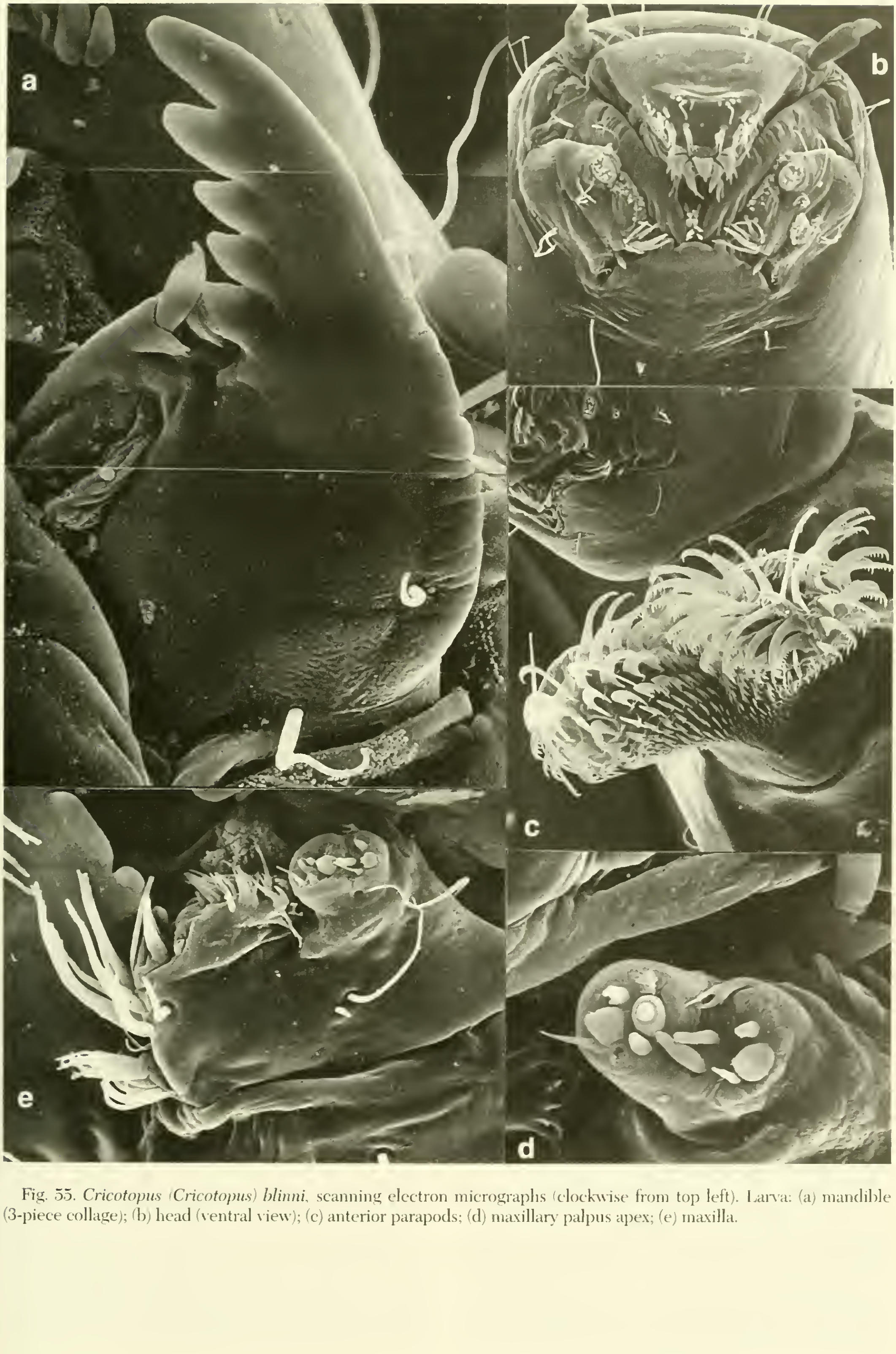

Fig. 55. *Cricotopus (Cricotopus) blinni*, scanning electron micrographs (clockwise from top left). Larva: (a) mandible (3-piece collage); (b) head (ventral view); (c) anterior parapods; (d) maxillary palpus apex; (e) maxilla.

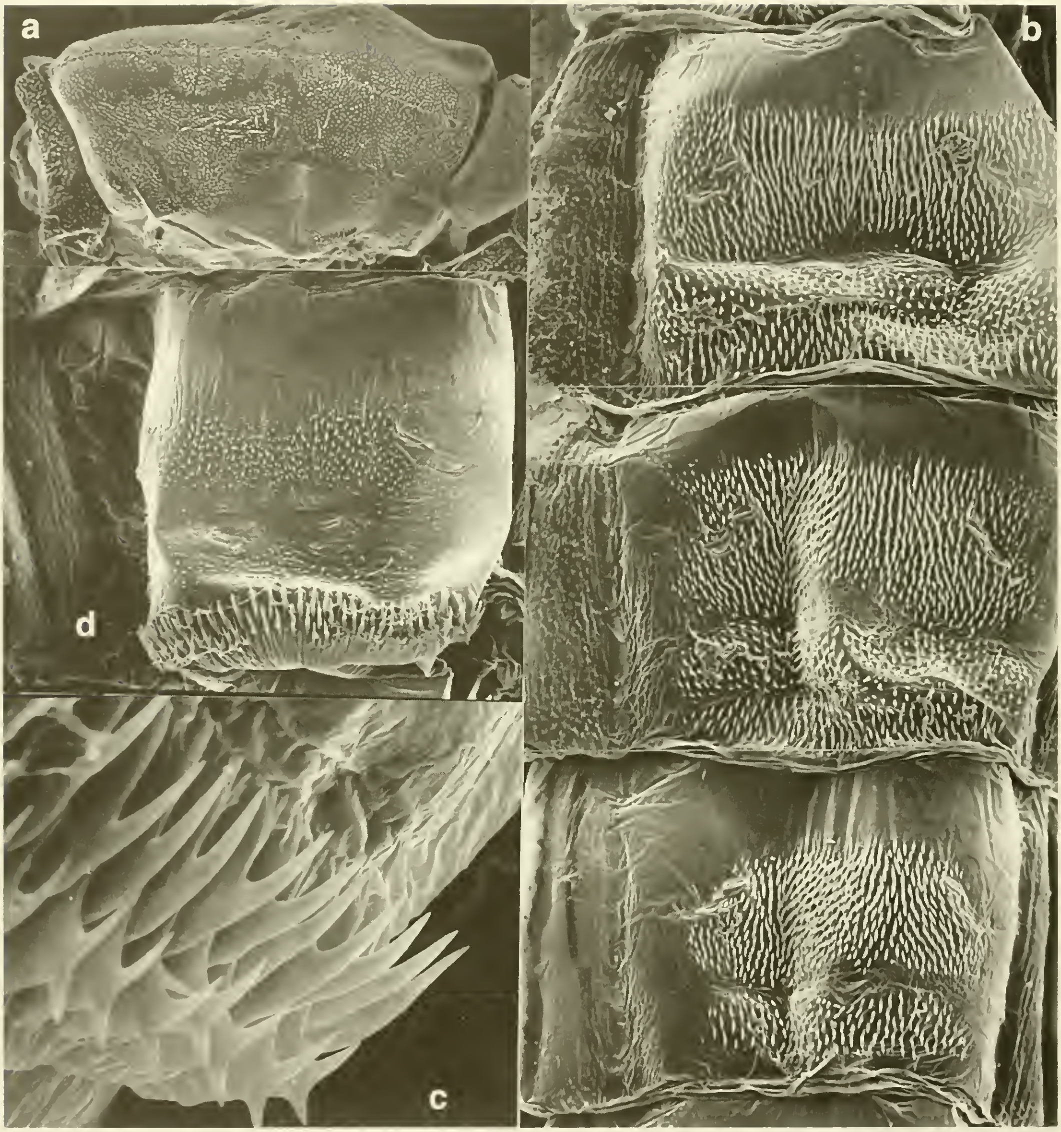

Fig. 56. *Cricotopus (Cricotopus) globistylus*, scanning electron micrographs (clockwise from top left). Male: (a) thorax (dorsolateral view). Pupa: (b) terga IV–VI (3-piece collage); (c) recurved hooks of tergum II; (d) tergum II.

Sublette and Sasa 1994: Fig. 188), thus providing a positive identification.

ECOLOGY AND DISTRIBUTION.—In Arizona this species has been collected in cold-stenothermic conditions in the Colorado River just below the Paria River.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 4 ♂, river mi 133.5, 610 m elev.

SUMMARY

The chironomid fauna of the Colorado River in Grand Canyon is depauperate in comparison with other North American rivers. Our sample of nearly 1500 larval, pupal, and adult chironomid specimens included 38 species in 23 genera and 4 subfamilies. The fauna was dominated by 23 species in the subfamily

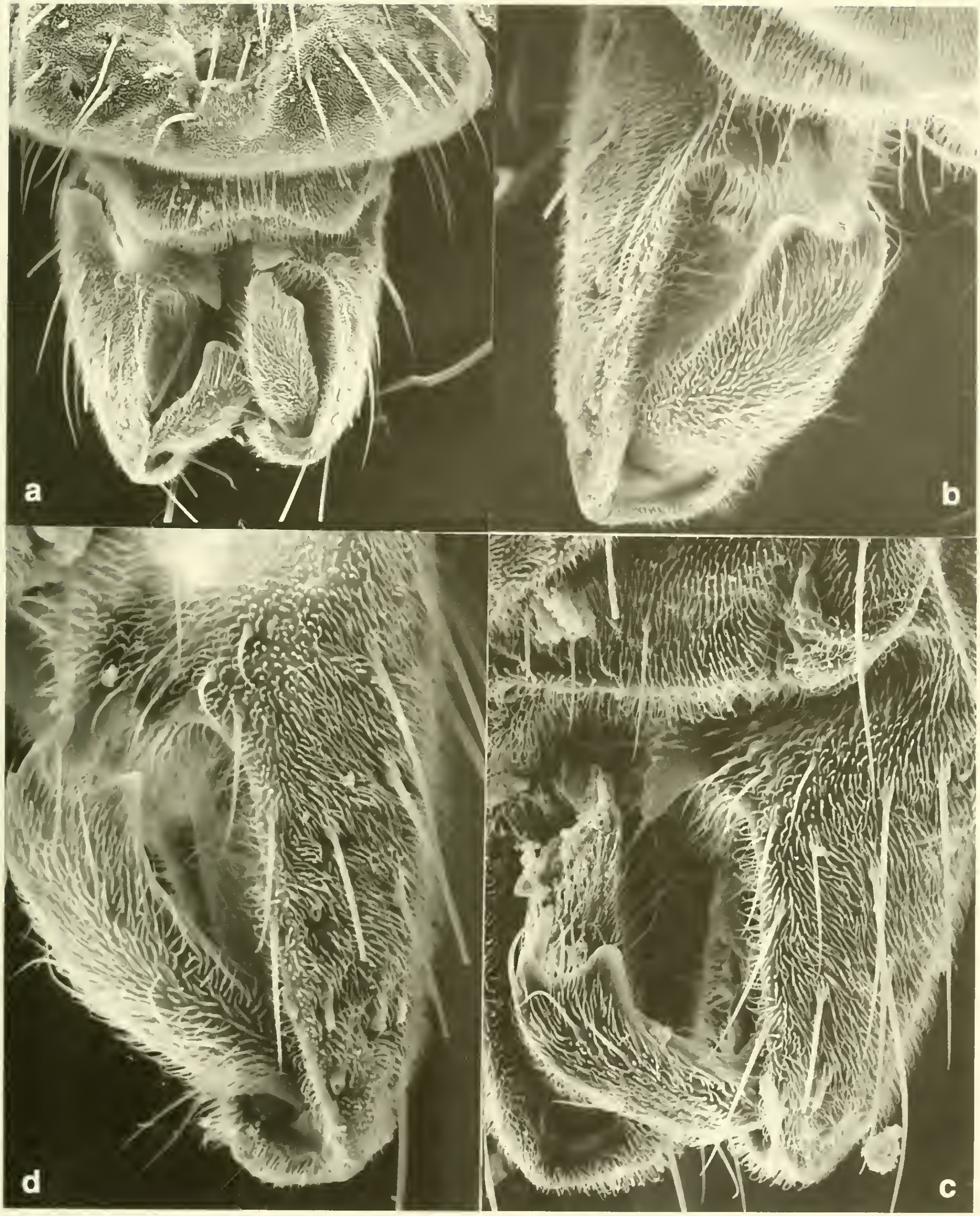

Fig. 57. *Cricotopus (Cricotopus) herrmanni*, scanning electron micrographs (clockwise from top left). Male: (a) genitalia; (b–d) gonostylus, positional variation.

Orthocladiinae, with *Cricotopus annulator* > *C. globistylus* > *Eukiefferiella claripennis* > *Orthocladius rivicola* > *Tvetenia vitracies*. *Chironomus* spp. (subfamily Chironominae) were regularly encountered in low densities in pool habitats floored with fine sediment. Twelve chironomine species were collected overall. *Procladius bellus*, *Paracladius conversus*, *Chironomus decorus*, *C.* sp. 1, and *C.* sp. 2 were collected only in the headwaters of Lake Mead.

Stevens et al. (1998) present a synthesis and summary of the Colorado River chironomid assemblage from the data presented here.

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CHIRONOMIDAE (DIPTERA) OF THE COLORADO RIVER, GRAND CANYON, ARIZONA, USA, II: FACTORS INFLUENCING DISTRIBUTION

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ABSTRACT.—Biogeographic, flow regulation (water clarity and temperature), and temporal influences affect the composition of the chironomid midge assemblage in the Colorado River between Glen Canyon Dam and Lake Mead. This assemblage is dominated by euryecious Nearctic and Holarctic orthocladine taxa (23 of 38 total species, total weighted relative abundance [WRA] = 0.972) and includes a minor Neotropical component. Chironomid species richness increases over distance downstream from the dam, and dominance shifts across 3 turbidity segments. Eleven species occur in the cold-stenothermic clearwater (CW) segment between the dam and the 1st perennial tributary (the Paria River, 26 km from the dam). Chironomid diversity increases from 18 to 24 species in the variably turbid (VT) and usually turbid (UT) segments downstream, respectively. Total *Cricotopus* spp. WRA is negatively correlated with distance (turbidity), while total Chironominae WRA shows the opposite pattern. In contrast to chironomid diversity, species density decreases from 0.42 species/km in the CW segment to 0.19 and 0.08 species/km in the VT and UT segments, respectively. Seasonal dominance shifts slightly from orthocladine *Eukiefferiella* spp. in winter (WRA = 0.101) to *Cricotopus* spp. (WRA = 0.165) in summer. Total WRA is lowest in spring (0.191). The assemblage is depauperate compared with other western rivers and has changed over post-dam time.

Key words: biodiversity, biogeography, Chironomidae, Colorado River, community, flow regulation, Glen Canyon Dam, Grand Canyon, serial discontinuity concept.

Chironomid midges play important roles in both aquatic and terrestrial food webs in river ecosystems. The Colorado River is one of the most thoroughly regulated American rivers (Hirsch et al. 1990), and chironomids are abundant or dominant taxa in many segments (Pearson 1967, Rader and Ward 1988, Wolz and Shiozawa 1995, Stevens et al. 1997). Virtually no pre-impoundment mainstream benthic data were collected (Blinn and Cole 1991). Following completion of Glen Canyon Dam in 1963, Stone and Rathbun (1967 unpublished) documented rapid changes in benthic macrophyte distribution at Lees Ferry, but reported the presence of only a single group of chironomids: ooze-dwelling "bloodworms" (Chironominae, probably *Chironomus* spp.). Sublette et al. (1998) identify 38 species of chironomids from the post-dam Colorado River in Glen and Grand canyons and discuss their autecology. These riverine Chironomidae link aquatic and terrestrial trophic components in Grand Canyon (Angradi 1994, Angradi and Kubly 1994a, 1994b, Blinn et al. 1995).

The Colorado River chironomid assemblage is influenced by biogeography (Sublette et al. 1998) as well as temporal and environmental factors, including flow regulation. However, detailed distributional data on individual chironomid species are rare, and phenology is well documented for rather few species. Hofnecht (1981) attributed low macroinvertebrate abundance in Grand Canyon tributary mouths to cold-stenothermic and fluctuating mainstream flows. Stevens et al. (1997) report that riffle and pool habitats in the clearwater segment immediately downstream from the dam support equally high densities of chironomid larvae in dense beds of the benthic alga *Cladophora glomerata*. In contrast, cobble bars in more turbid downstream segments support substantially greater chironomid abundance than do mainstream pool habitats. Chironomid species richness is low downstream from Glen Canyon Dam (Sublette et al. 1998), but other factors influencing diversity, such as seasonal phenology and impoundment impacts on water clarity, have not been analyzed.

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In this paper we synthesize taxonomic and ecological data of Sublette et al. (1998) to describe factors influencing the chironomid assemblage of the Colorado River between Glen Canyon Dam and Lake Mead. We use data from preserved pharate and adult chironomid specimens collected from 1974 through 1991 to describe biogeography, spatial and temporal distribution, and influences of flow regulation on this assemblage. Our results provide the first quantitative description of the chironomid assemblage in this portion of the Colorado River and establish a baseline for monitoring future change in these assemblages.

METHODS AND MATERIALS

Study Area

The channel of the Colorado River between Glen Canyon Dam and Lake Mead is constrained by talus slopes and bedrock. The river descends from an elevation of 955 m to 370 m over its 472-km-long course through Sonoran and Mohave Desert terrain (Warren et al. 1982). By convention, distances along the river are measured from Lees Ferry (river km and mi 0, 25 km downstream from the dam; Sublette et al. 1998: Fig. 1). The pre-dam mean daily flow ranged from <100 to >2500 m^3/s (Howard and Dolan 1981), with a spring snowmelt peak flow, erratic summer flows, and low winter flows. Pre-impoundment flows transported more than 60×10^6 mt/yr of inorganic sediment (Andrews 1991), and undoubtedly much organic drift. Water temperatures ranged from 0°C in winter to ≥29.4°C at Lees Ferry in summer before completion of the dam. The river channel is constricted by debris fans at the confluences of >500 mostly ephemeral tributaries. Runs, riffles or rapids, pools, and backwaters are primary river habitats, and their distribution varies through 13 bedrock-defined reaches (Schmidt and Graf 1990, Stevens et al. 1995, 1997).

Completion of Glen Canyon Dam in 1963 reduced effects of regional climate on the Colorado River and altered chironomid habitat availability. The post-impoundment hydrograph has been characterized by large hourly, but relatively minor seasonal, flow variability (Howard and Dolan 1981, U.S. Bureau of Reclamation 1995). Between 1963 and 1991, hourly flow variation for hydroelectric power production created daily "tides" of ≥3 m that inundated or desiccated shoreline habitats (Blinn et al. 1995). Seasonal thermal variability has been replaced by cold-stenothermic (hypolimnetic) flow releases (8–9°C) at Lees Ferry, and water temperature increases to only 17°C at Diamond Creek (km 364, mi 226) in summer (Stevens et al. 1997). Stabilized flows permit widespread establishment of aquatic, wetland, and riparian vegetation (Stone and Rathbun 1967 unpublished, Turner and Karpiscak 1980, Johnson 1991, Stevens et al. 1995), which serve as chironomid habitat. Sediment retention in Lake Powell increases water clarity in lower Glen Canyon; however, the Paria River (km 1, mi 0.7), Little Colorado River (km 98, mi 61), and other tributaries supply exceptionally concentrated suspended sediment loads (Andrews 1991, Graf et al. 1991). These tributaries create 3 turbidity segments: the 26-km-long clearwater (CW) segment from the dam to the Paria River confluence, the variably turbid (VT) segment from the Paria River and Little Colorado River mouth, and the usually turbid (UT) segment (km 98 to km 386, mile 240). In addition, upper Lake Mead (ULM) constitutes a usually turbid, lacustrine segment from km 386 to km 442 (mi 278).

Field and Analytical Methods

We collected adult and pharate aquatic Diptera throughout the year in 1976–77 and 1989–92 by sweep-netting riparian vegetation (particularly *Salix exigua*, *Tamarix ramosissima*, and *Baccharis* spp.), white- and UV light-trapping, dip-netting, and larval rearing from benthic spot and quantitative samples (Sublette et al. 1998). Taxonomic determinations and descriptions follow Sublette et al. (1998), which also includes additional information on collection methods, locations of specimens, and taxonomy.

We conducted spatial and seasonal analyses using data from 1018 slide-mounted pharate and adult specimens from 212 samples collected throughout the study area by Stevens (1976) from 1974 to 1976, and from 1989 through 1992. Up to 10 specimens of visually apparent species from each sample were slide-mounted for identification. Twenty samples were collected from the CW segment, 76 from the VT segment, 113 from the UT segment, and 3 from the ULM segment. Because few samples were collected in the last segment, we pooled ULM data with UT data. We sampled

Chironomidae throughout the year, with 54 samples collected in winter (December–February), 62 in spring (March–May), 47 in summer (June–August), and 49 in autumn (September–November).

By weighting the relative abundance of each species in relation to the number of samples collected in each turbidity segment, we standardized spatial distribution of adult chironomids. Species density was calculated by dividing the number of species in a turbidity segment by segment length (km). Seasonal variation was standardized by weighting each species' relative abundance by the number of collections made each season.

RESULTS AND DISCUSSION

Composition

The chironomid fauna of the Colorado River in Grand Canyon is depauperate in comparison with other western rivers (e.g., Sublette and Sublette 1979, Wolz and Shiozawa 1995, Spindler 1996). Our collections include 38 species in 23 genera and 4 subfamilies (Table 1). The fauna is dominated by the Orthocladiinae (23 species), with 5 abundant species: *Cricotopus annulator* > *Cricotopus globistylus* > *Eukiefferiella claripennis* > *Orthocladius rivicola* > *Tvetenia vitracies*. The fauna includes 12 Chironominae species, with *Chironomus* spp. regularly found in low densities in pool and backwater habitats floored with fine sand or silt, and with *Procladius bellus, Paracladius conversus, Chironomus decorus, C.* sp. 1, and *C.* sp. 2 collected only in the ULM segment.

Spindler (1996) reports at least 43 chironomid taxa in 38 genera from 10 Grand Canyon tributary streams, adding 20 genera to our list, for a total of 43 genera in Grand Canyon. Thus, more chironomid species may exist in tributary streams than in the mainstream Colorado River. Cowley (1995 unpublished) reports 172 chironomid species or taxa in the highly regulated Rio Grande in New Mexico, 4.5 times as many species as we encountered in the Colorado River mainstream.

Biogeography

Nine of the 38 species collected in the mainstream Colorado River are Holarctic in distribution and are madicolous or aufwuchs feeders (Sublette et al. 1998). All are Orthocladiinae, and the other orthocladines in this system also probably share this feeding strategy. The Orthocladiinae are primarily cool- or coldwater taxa, and their dominance in the Colorado River is not surprising because the river is now a cold-stenothermic stream, and because proximity to cold, high-elevation habitats provides a regional species pool of potential colonists. In contrast, the subfamily Chironominae, which largely consists of warmwater species, is represented by low densities of *Chironomus utahensis* and *C. decorus* in fine-grained habitats. A small Neotropical component is represented by *Polypedilum obelos* and *Rheotanytarsus hamatus*, which previously had been reported only from Guatemala (Sublette and Sasa 1994).

The depauperate condition of the Grand Canyon midge fauna may be explained partially by biogeographic constraints. Ecological isolation within this large, canyon-bound, desert river may have restricted pre-impoundment chironomid colonization. Colonization may have been restricted by the distance from source areas and by large annual ranges of water and air temperatures. Also, the combination of frequent large floods and high suspended and bed-transported sediment loads may have reduced pre-impoundment ecological heterogeneity, and therefore diversity. Coffman (1989) reviewed chironomid diversity in 152 stream studies, concluding that stream size and biogeographic potential, as well as ecological heterogeneity, altitude, and latitude, influence chironomid diversity. He reported the greatest chironomid diversity in medium-sized streams. Thus, the large, isolated, flood-prone, seasonally warm pre-impoundment Colorado River simply may not have supported many chironomid species. Polhemus and Polhemus (1976) similarly attribute the depauperate condition of the aquatic and semiaquatic Hemiptera fauna in Grand Canyon to biogeographic isolation; however, this argument may not apply as strongly to the Chironomidae because of adult dispersal as "aerial plankton."

Spatial Distribution Within the Study Area

The chironomid assemblage changes over distance from Glen Canyon Dam, through increasingly more turbid segments (Table 1). The CW segment supports the highest reach total weighted relative abundance (WRA = 0.471). The CW assemblage is strongly dominated by Orthocladiinae (0.468), particularly

TABLE 1. Sample-weighted relative abundance of adult Grand Canyon Chironomidae in 3 turbidity segments of the Colorado River downstream from Glen Canyon Dam.

	Turbidity Segments			
Taxa	Clearwater ($n = 20$)	Variably turbid ($n = 76$)	Usually turbid ($n = 116$)	Total ($n = 212$)
TANYPODINAE				
Procladius bellus	0.000	0.000	0.001	0.001
DIAMESINAE				
Diamesia heteropus	0.000	0.001	0.000	0.001
ORTHOCLADIINAE				
Cardiocladius platypus	0.003	0.002	0.003	0.007
Cricotopus annulator	0.173	0.087	0.044	0.303
Cricotopus blinni	0.000	0.000	0.003	0.003
Cricotopus globistylus	0.181	0.003	0.001	0.185
Cricotopus herrmanni	0.000	0.005	0.001	0.006
Cricotopus infuscatus	0.000	0.000	0.006	0.006
Cricotopus trifacsia	0.003	0.008	0.012	0.023
Undet. *Cricotopus* sp.	0.000	0.001	0.001	0.001
Subtotal *Cricotopus* spp.	0.357	0.103	0.067	0.527
Eudactylocladius dubitatus	0.000	0.000	0.000	0.000
Eukiefferiella claripennis	0.038	0.039	0.060	0.137
Eukiefferiella coerulescens	0.009	0.004	0.006	0.018
Eukiefferiella ilkleyensis	0.012	0.028	0.016	0.055
Undet. *Eukiefferiella* sp.	0.000	0.002	0.009	0.011
Subtotal *Eukiefferiella* spp.	0.059	0.073	0.090	0.221
Undet. *Limnophyes* sp.	0.000	0.000	0.001	0.001
Metriocnemus stevensi	0.000	0.002	0.000	0.002
Orthocladius frigidus	0.000	0.000	0.000	0.000
Orthocladius lutipes	0.000	0.001	0.000	0.001
Orthocladius mallochi	0.000	0.000	0.001	0.001
Orthocladius rivicola	0.032	0.049	0.033	0.114
Undet. *Orthocladius* sp.	0.000	0.001	0.002	0.003
Subtotal *Orthocladius* spp.	0.032	0.051	0.035	0.118
Paracladius conversus	0.000	0.000	0.001	0.001
Parakiefferiella subaterrima	0.000	0.000	0.002	0.002
Parametriocnemus lundbeckii	0.000	0.000	0.001	0.001
Paraphaenocladius exagitans	0.000	0.001	0.000	0.001
Pseudosmittia nanseni	0.003	0.000	0.000	0.003
Undet. *Pseudosmittia* sp.	0.000	0.000	0.000	0.001
Tvetenia vitracies	0.015	0.042	0.032	0.089
Total Orthocladiinae	0.468	0.274	0.230	0.972
CHIRONOMINAE				
Chironomini				
Apedilum subcinctum	0.000	0.001	0.000	0.001
Chironomus decorus	0.000	0.000	0.003	0.003
Chironomus utahensis	0.003	0.002	0.000	0.004
Chironomus sp. 1	0.000	0.000	0.001	0.001
Chironomus sp. 2	0.000	0.000	0.001	0.001
Cyphonella gibbera	0.000	0.000	0.002	0.002
Phaenospectra profusa	0.000	0.000	0.001	0.002
Polypedilum apicatum	0.000	0.000	0.001	0.001
Polypedilum obelos	0.000	0.000	0.002	0.004
Undet. *Polypedilum* sp.	0.000	0.000	0.001	0.001
Tanytarsini				
Cladotanytarsus marki	0.000	0.000	0.006	0.006
Rheotanytarsus hamatus	0.000	0.000	0.003	0.003
Undet. *Micropsectra* sp.	0.000	0.000	0.000	0.000
Total Chironominae	0.003	0.006	0.018	0.027
GRAND TOTAL	0.471	0.281	0.248	1.000
TOTAL SPECIES RICHNESS	11	18	24	38
SPECIES DENSITY (species/km)	0.42	0.19	0.08	

Cricotopus (genus total WRA = 0.357), with *C. globistylus* (0.181) and *C. annulator* (0.173) most abundant. *Eukiefferiella* spp. (genus total WRA = 0.059), particularly *E. claripennis* (0.038), and 8 other species are subdominant in the CW segment. The river floor substrata in the CW segment has changed from primarily sand to primarily cobble in post-dam time (Howard and Dolan 1981). Benthic cobbles have been colonized by *Cladophora glomerata*, a filamentous green alga that supports abundant epiphytic diatoms on which chironomid larvae feed (Hardwick et al. 1992, Blinn et al. 1995), and more recently by additional macrophyte taxa.

Downstream from the confluence of the small but extremely turbid Paria River the chironomid assemblage undergoes a 3.5-fold reduction in total WRA of *Cricotopus* spp., with low-density co-dominance by *C. annulator*, *Eukiefferiella claripennis*, *Orthocladius rivicola*, and *Tvetenia vitracies* (Table 1). Low chironomid standing stock biomass (Stevens et al. 1997), low WRA values (<0.061), and continued co-dominance of these species (except *Tvetenia vitracies*) also characterize the UT segment in lower Grand Canyon. Chironomid diversity increases from the CW (11 species) to the VT segment (18 species) to the UT (24 species); however, species density decreases from 0.43 spp./km to 0.19 spp./km and 0.08 spp./km through these turbidity segments, respectively.

Similarity with Other Western Rivers

Similarity between the Grand Canyon chironomid assemblage and that in other portions of the Colorado River or in other western rivers is negatively related to distance from our study area. Eighteen of 38 chironomid genera reported by Spindler (1996) in Grand Canyon tributaries also occur in the Colorado River mainstream; however, additional sampling of other tributaries, seeps and springs, and canyon rim wetlands is needed to provide a more complete understanding of chironomid diversity in Grand Canyon.

The post-impoundment Colorado River in Grand Canyon supports habitats and chironomid species that also occur in the upper and middle Green River, 600 km upstream. Wolz and Shiozawa (1995) report 19 genera of Chironomidae in Ouray National Wildlife Refuge, Utah, in low-velocity environments, including *Chironomus*, *Cricotopus*, *Cryptochironomus*, *Polypedilum*, *Procladius*, *Tanypus*, and *Tanytarsus*. Chironomid density there ranges up to 31,125/m^2 in river backwaters, an order of magnitude greater than that in the mainstream. The Grand Canyon portion of the Colorado River also contains numerous backwaters; however, steep gradients and swift currents limit fine-sediment deposition. Consequently, chironomid densities (primarily *Chironomus* spp.) in contemporary Grand Canyon backwaters are typically <1000/m^2 (Stevens unpublished data). Chironomids in the Colorado River in Grand Canyon are often more concentrated in cobble bar habitats, which are relatively rare on the sand-floored Green River. Habitat availability and biogeograhic constraints are probably responsible for assemblage variation between the 2 study areas.

Cowley (1995 unpublished) describes chironomid assemblages in the Rio Grande in New Mexico using Ward's (1963) clustering algorithm. He reports a total of 172 species that can be categorized into 3 distinct clusters. The 1st cluster includes 19 "widespread species," of which 8 also occur in Grand Canyon. His 2nd cluster comprises cold, cleanwater species and shares 9 species in common with the Grand Canyon fauna. His 3rd cluster includes species of lower elevations and shares 7 species in common with the Grand Canyon fauna. Five of the remaining 13 species from Grand Canyon could not be identified to species level because of poor preservation but probably also occur in New Mexico as members of the 3rd cluster. Thus, at least 24 (14%) of the Rio Grande chironomids co-occur on the Colorado River mainstream, a relatively small amount of faunal overlap when compared to the compositional overlap at other locations within the Colorado River basin.

Flow Regulation Impacts

The serial discontinuity concept (SDC; Ward and Stanford 1983) predicts that macroinvertebrate diversity decreases following impoundment, but increases with distance downstream from large dams on large rivers. The depauperate midge diversity in Grand Canyon generally supports the predictions of that model and reflects impoundment influences of cold-stenothermic release temperatures and fluctuating flows (Blinn et al. 1995). Water temperature during prepupal and pupal development influences chironomid emergence, at least for arctic lentic chironomids (Danks and Oliver 1972, Welch 1973, Butler 1980), and seasonal warming cues larval development (Ward and Stanford 1982). Although the CW segment supports extremely high benthic standing biomass, only those species capable of tolerating cold-stenothermic conditions can persist there. Taxa we report there are primarily euryecious Nearctic or Holarctic Orthocladiinae, with relatively large body sizes (e.g., *Cricotopus* spp.). The great abundance but low diversity of chironomid species in the CW segment reflects the large standing stock biomass of epiphytic algae and relatively high productivity (Blinn et al. 1995, Stevens et al. 1997). The negative correlation between chironomid species density (as the number of species/km) and distance downstream does not follow SDC predictions, suggesting that the SDC may be refined by additional study of species/area biogeographic influences.

Potential niche diversity (as the range of available types of niches) increases downstream in Grand Canyon through increased seasonal variation in water temperature, increased size and abundance of backwaters in wide reaches, variation in benthic algal composition, increased organic drift from tributaries and allocthonous sources, and increased variability of other ecological gradients (Schmidt and Graf 1990, Shannon et al. 1996). Dominance shifts from a lower diversity of larger-bodied *Cricotopus* spp. in the upstream clearwater segment to an assemblage dominated by smaller-bodied madicolous taxa (e.g., *Eukiefferiella* spp.), with lower abundance and species density in downstream reaches. This pattern is at least partially attributable to turbidity (distance)-related reduction in aquatic macrophyte standing biomass, which provides abundant food and habitat upstream. Dam impacts on temperature limit invertebrate diversity, while water clarity limits benthic standing biomass in this system.

Cowley (1995 unpublished) examines the similarity of chironomid assemblages in regulated and unregulated reaches of the Rio Grande in New Mexico, reporting 5 groups of sites (4 clusters and 1 outlier site). His least perturbed (outlier) site on the Chama River supports 76 species, of which 22 occur only at that site. One group of sites on the Chama River contains 2 stations downstream from dams. Those sites have high mean diversity (41 species/site) but, on average, only 4 unique species per site. A 2nd cluster, representing moderate to low water quality, has a mean of only 25 species with a mean of only 2 unique species per site. The diversity pattern in this cluster resembles that in our study area; however, Colorado River water quality is relatively high. In contrast to our study, Cowley reports that Chama River chironomid diversity is negatively correlated with distance downstream from Abiquiu Dam, with highest midge diversity at the coldest station just downstream from the dam.

Sublette and Sublette (1979) compare the Chironomidae from regulated and unregulated sites on the Navajo River above Navajo Dam and on the San Juan River at Farmington, New Mexico, about 65 km downstream from the dam. They report 67 species at the above-dam site and 56 below the dam, just downstream from the Animas River confluence at Farmington, New Mexico. The above-dam site is comparable to Cowley's least perturbed site on the Chama River, while the assemblage below the dam resembles his 1st cluster on the Chama River. The influence of that relatively large tributary restores water temperature variability and may explain the similarity of chironomid diversity above and below the impoundment. No tributary entering the Grand Canyon portion of the Colorado River is large enough to restore mainstream temperature, and flow regulation impacts on temperature persist throughout the entire study area (Stevens et al. 1997).

Hourly flow fluctuations in Grand Canyon affect chironomid diversity by regularly inundating or desiccating large portions of the shoreline (Blinn et al. 1995). We observed, but did not quantify, rapid emergence of *Cricotopus* and other chironomids from *Cladophora glomerata* beds exposed by fluctuating flows.

Temporal Variation

The chironomid assemblage in Grand Canyon changes only slightly between seasons but has shifted over post-dam time (Table 2). Chironomid diversity increases from 17 species in winter and spring to 22 and 21 species in summer and autumn, respectively. Spring, summer, and autumn assemblages are dominated by *Cricotopus* spp. (genus WRA = 0.076, 0.165, and 0.114, respectively), particularly *C. annulator*. Winter dominance shifts to *Eukiefferiella*

TABLE 2. Seasonal sample-weighted relative abundance of adult Grand Canyon Chironomidae downstream from Glen Canyon Dam: winter (December–February), spring (March–May), summer (June–August), autumn (September–November).

	Season				
Taxa	Winter ($n = 54$)	Spring ($n = 62$)	Summer ($n = 47$)	Autumn ($n = 49$)	Total ($n = 212$)
TANYPODINAE					
Procladius bellus	0.000	0.000	0.001	0.000	0.001
DIAMESINAE					
Diamesia heteropus	0.000	0.000	0.000	0.001	0.001
ORTHOCLADIINAE					
Cardiocladius platypus	0.003	0.003	0.001	0.001	0.008
Cricotopus annulator	0.013	0.049	0.114	0.086	0.262
Cricotopus blinni	0.001	0.000	0.001	0.003	0.005
Cricotopus globistylus	0.011	0.017	0.030	0.009	0.067
Cricotopus herrmanni	0.000	0.007	0.000	0.000	0.007
Cricotopus infuscatus	0.003	0.001	0.006	0.002	0.011
Cricotopus trifacsia	0.006	0.003	0.014	0.014	0.036
Undet. *Cricotopus* sp.	0.000	0.001	0.001	0.000	0.002
Subtotal *Cricotopus* spp.	0.034	0.076	0.165	0.114	0.389
Eudactylocladius dubitatus	0.000	0.000	0.000	0.000	0.000
Eukiefferiella claripennis	0.058	0.041	0.021	0.055	0.175
Eukiefferiella coerulescens	0.008	0.005	0.002	0.003	0.018
Eukiefferiella ilkleyensis	0.023	0.021	0.019	0.005	0.067
Undet. *Eukiefferiella* sp.	0.012	0.003	0.003	0.002	0.020
Subtotal *Eukiefferiella* spp.	0.101	0.070	0.045	0.065	0.280
Undet. *Limnophyes* sp.	0.001	0.000	0.000	0.000	0.001
Metriocnemus stevensi	0.000	0.001	0.001	0.000	0.002
Orthocladius frigidus	0.000	0.000	0.000	0.000	0.000
Orthocladius lutipes	0.000	0.000	0.001	0.000	0.001
Orthocladius mallochi	0.000	0.001	0.000	0.000	0.001
Orthocladius rivicola	0.071	0.017	0.034	0.015	0.136
Undet. *Orthocladius* sp.	0.004	0.001	0.000	0.000	0.005
Subtotal *Orthocladius* spp.	0.075	0.018	0.035	0.015	0.143
Paracladius conversus	0.000	0.000	0.000	0.002	0.002
Parakiefferiella subaterrima	0.001	0.001	0.000	0.001	0.003
Parametriocnemus lundbeckii	0.000	0.000	0.001	0.000	0.001
Paraphaenocladius exagitans	0.000	0.000	0.000	0.001	0.001
Pseudosmittia nanseni	0.000	0.001	0.000	0.000	0.001
Undet. *Pseudosmittia* sp.	0.000	0.000	0.001	0.000	0.001
Tvetenia vitracies	0.033	0.021	0.007	0.060	0.120
Total Orthocladiinae	0.248	0.190	0.256	0.259	0.953
CHIRONOMINAE					
Chironomini					
Apedilum subcinctum	0.000	0.000	0.000	0.001	0.001
Chironomus decorus	0.000	0.001	0.002	0.002	0.005
Chironomus utahensis	0.001	0.000	0.002	0.000	0.003
Chironomus sp. 1	0.000	0.000	0.000	0.002	0.002
Chironomus sp. 2	0.000	0.000	0.000	0.001	0.001
Cyphomella gibbera	0.002	0.000	0.001	0.000	0.003
Phaenospectra profusa	0.003	0.000	0.000	0.000	0.003
Polypedilum apicatum	0.000	0.000	0.001	0.001	0.002
Polypedilum obelos	0.006	0.000	0.000	0.000	0.006
Undet. *Polypedilum* sp.	0.001	0.000	0.001	0.000	0.002
Tanytarsini					
Cladotanytarsus marki	0.000	0.000	0.002	0.009	0.012
Undet. *Micropsectra* sp.	0.000	0.000	0.000	0.000	0.000
Rheotanytarsus hamatus	0.000	0.000	0.006	0.000	0.006
Total Chironominae	0.012	0.001	0.015	0.017	0.045
GRAND TOTAL	0.260	0.191	0.272	0.277	1.000
TOTAL SPECIES RICHNESS	17	17	22	21	38

(genus WRA = 0.101), particularly *E. claripennis* (winter WRA = 0.058), and *Orthocladius* spp. (genus WRA = 0.075), especially *O. rivicola* (WRA = 0.071). Adult *Tvetenia vitracies* are common from autumn through spring (0.06–0.021) and rare in summer (0.007).

The pre-impoundment river was characterized by large late spring or early summer floods. If non-*Cricotopus* Orthocladiinae characterized the pre-impoundment river, their phenology may reflect avoidance of spring and summer floods, with oviposition on the descending, warming, or autumn limbs of the hydrograph. Increased environmental constancy (unithermal releases and reduced flooding disturbance) and a shift in benthic substrata from silt/sand to cobble (Howard and Dolan 1981) favor species that apparently do not require warming cues and may emerge throughout the year (e.g., some *Cricotopus* spp.). As some thermal and substrate conditions are restored over distance downstream, total Chironominae WRA increases from 0.003 to 0.018 (Table 1).

The Colorado River chironomid assemblage has changed during post-dam time. Stone and Rathbun (1967 unpublished) noted only "blood worms" (probably *Chironomus* spp.) among numerous aquatic invertebrate collections at Lees Ferry immediately after impoundment. Identification of 49 adult specimens collected by Stevens (1976) in 1975 at Lees Ferry reveals an assemblage dominated by small-bodied *Cladotanytarsus* sp., *Tvetenia vitracies*, and *Apedilum subcinctum*, a species not collected subsequently. A total of 14 species collected there from 1990 to 1992 show strong dominance by *Cricotopus* spp. This chironomid assemblage is likely to continue to change through time as colonization occurs from tributaries and riverside springs, as extinction occurs, and in response to dam management policies.

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SPOTTED KNAPWEED DISTRIBUTION IN STOCK CAMPS AND TRAILS OF THE SELWAY-BITTERROOT WILDERNESS

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ABSTRACT.—This article documents spotted knapweed (*Centaurea maculosa* Lam.) in 30 campsites and along 5 trails in the Selway-Bitterroot Wilderness and assesses the role of disturbance and environmental factors in controlling infestation. Spotted knapweed was present in only 6 of 30 surveyed campsites and limited portions of all 5 trails that were sampled. All spotted knapweed in camps was below 1700 m elevation, in open canopy, and in areas with an opportunity class disturbance ranking of 3 or 4. Overall disturbance levels measured using U.S. Forest Service Site Impact Worksheets (SIWs) did not help predict occurrence of spotted knapweed, although bare mineral soil, vegetation loss, and development variables of SIWs provide some explanation of spotted knapweed presence or absence. There was no significant difference in knapweed frequency between areas used predominantly by horses and those used by humans within camps. Over 95% of spotted knapweed along trails was found within 0.5 km of the trailhead, occurred within 4.6 m of the trail, and had low reproductive potential. If the Bitterroot portion of the Selway-Bitterroot Wilderness is representative of forested wilderness areas in the Northern Rockies, then the perceived threat of spotted knapweed to wilderness areas may substantially exceed the actual danger in many instances. Study findings indicate that managers should conduct surveys before initiating costly control measures in wilderness areas, that eradication may be a viable alternative when spotted knapweed numbers are this low, and that regulations promoting minimum-impact camping should reduce spotted knapweed infestation.

Key words: spotted knapweed, wilderness, management, disturbance, camp, trail.

Exotic plants pose a threat to wilderness areas where they displace native species and alter natural conditions that wilderness areas are intended to preserve (Kummerow 1992). Management policies on these public lands now call for control of nonnative species to preserve native plant communities (Westman 1990). Despite these policies, recent studies have shown ever-increasing numbers of nonnative species in public lands of the Northern Rocky Mountain region (Losensky 1987, Lolo National Forest 1991, Whipple 1991, Tyser and Worley 1992, Flathead National Forest 1993, Lesica et al. 1993).

One of the most pernicious exotic species is spotted knapweed (*Centaurea maculosa* Lam.), which covers vast areas of the American West. This species is thought to be actively invading the Selway-Bitterroot Wilderness Area of Montana and Idaho (Losensky 1987). Understanding the mechanisms that allow invasion of spotted knapweed into this large wilderness area provides insights to the problem and guidance on means of controlling this species in a variety of wilderness settings. This article documents the extent of spotted knapweed along trails and in stock camps in the Bitterroot portion of the Selway-Bitterroot Wilderness and evaluates the role of disturbance and environmental factors in controlling its extension in this area.

SPOTTED KNAPWEED HABITAT AND STUDY AREA

Spotted knapweed is native to the steppes of Europe. Introduced to North America in the early 20th century as a contaminant in Turkestan alfalfa (*Medicago sativa* L.) seed (Groh 1940), it has, since that time, expanded its range to cover almost 3 million ha in the northwest United States (Lacey et al. 1992).

Spotted knapweed in Montana has been found in areas where average annual precipitation is as low as 200 mm/yr and as high as 2030 mm/yr (Lacey et al. 1992), although Chicoine et al. (1985) found most spotted knapweed in areas with average annual precipitation between 310 and 760 mm/yr. Survival and reproduction are enhanced if precipitation coincides with seedling emergence (Schirman

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1981), and germination increases with increased soil moisture content (Spears et al. 1980). Soil type, however, does not appear to play a major role in determining spotted knapweed distribution (Schirman 1984).

Optimum temperatures for germination are between 10°C and 28°C (Chicoine 1984), and the plant seems best adapted to areas with 90–120 frost-free days (Chicoine et al. 1985). Spotted knapweed in Montana has been documented at elevations from 579 m to 3048 m, with 90% of infested rangeland sites occurring between 610 m and 1829 m (Lacey et al. 1992). Spotted knapweed occupies every major habitat type west of the Continental Divide in Montana (Mooers and Willard 1989), although on forested lands it is believed to pose the greatest threat in the relatively low-lying ponderosa pine (*Pinus ponderosa* Doug.) and Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) habitats (Forcella and Harvey 1983, Losenky 1987).

Disturbed habitat is a key factor facilitating spotted knapweed invasion. Exposed soil, reduced canopy, irrigation, selective grazing of native species, and contaminated hay all have been cited as causative factors in the spread of spotted knapweed (Watson and Renney 1974, Morris and Bedunah 1984, Mooers 1986, Losensky 1987).

Dispersion of Spotted Knapweed

Spotted knapweed reproduces only by seed (Story 1992) and disperses naturally through peripheral enlargement (Watson and Renney 1974). Seeds are dispersed up to 1 m by a flicking motion when the plant is disturbed. In Montana seed production of spotted knapweed averages 1000 seeds per plant (Chicoine 1984). French and Lacy (1983) found that seeds may remain viable for up to 5 yr, while Davis et al. (1993) continued to find viable seeds into the 8th yr of their study.

Spotted knapweed rapidly expands along roadways and in fields as plants are caught up in the undercarriage of farm machinery and motor vehicles (Montana Department of Agriculture 1986, Lacey et al. 1992). In preserves and grasslands, primary roads and motor vehicles help facilitate seed dispersal into adjacent grasslands and trailheads (Tyser and Worley 1992). Within wilderness stock camps, where use of motorized vehicles is prohibited, spotted knapweed can be introduced from seeds in pack stock hay (Cole 1983, Marion et al. 1986) or within manure from animals that have consumed weed-infested feed (Dale and Weaver 1974, Marion et al. 1986, Montana Department of Agriculture 1986). Seeds can also adhere to damp tarp or tent bottoms or become attached to humans or pack stock as they move along trails (Watson and Renney 1974, Marion et al. 1986). Stock camps are occupied by both humans and animals, but usually pack and saddle stock are kept separate from the portion of the camp where humans eat, sleep, and socialize. Thus, one might expect more spotted knapweed to be present in stock portions of the camp.

Early work suggested that spotted knapweed is allelopathic (Chicione 1984), but later research by Kelsey and Bedunah (1989) found that allelopathy is not a significant factor contributing to the spread of spotted knapweed. Harvey and Nowierski (1989), however, documented the possibility of spotted knapweed displacing other species by depleting the soil of phosphorus and other nutrients.

OBJECTIVES AND HYPOTHESES

This study documents spotted knapweed distributions in camp sites and along trails to determine the role of disturbance and select environmental variables in controlling the presence and abundance of spotted knapweed in the Selway-Bitterroot Wilderness. Specifically, we evaluate the hypotheses that spotted knapweed abundance will (1) decrease at higher elevations, (2) increase in areas with open canopy cover, (3) be greater in areas with higher Forest Service disturbance rankings and (4) be higher in stock than in human portions of camp sites. The number of viable spotted knapweed seeds within 3 km of trailheads is also documented to assess the reproductive potential of plants.

The primary objective of this work was to provide resource managers with an improved understanding of (1) the extent of spotted knapweed infestations in the Selway-Bitterroot Wilderness Area, (2) controls on spotted knapweed distribution in Northern Rocky wilderness settings, and (3) possible management approaches for dealing with this problem.

STUDY AREA

We chose the Bitterroot segment of the Selway-Bitterroot Wilderness (Fig. 1) as a study

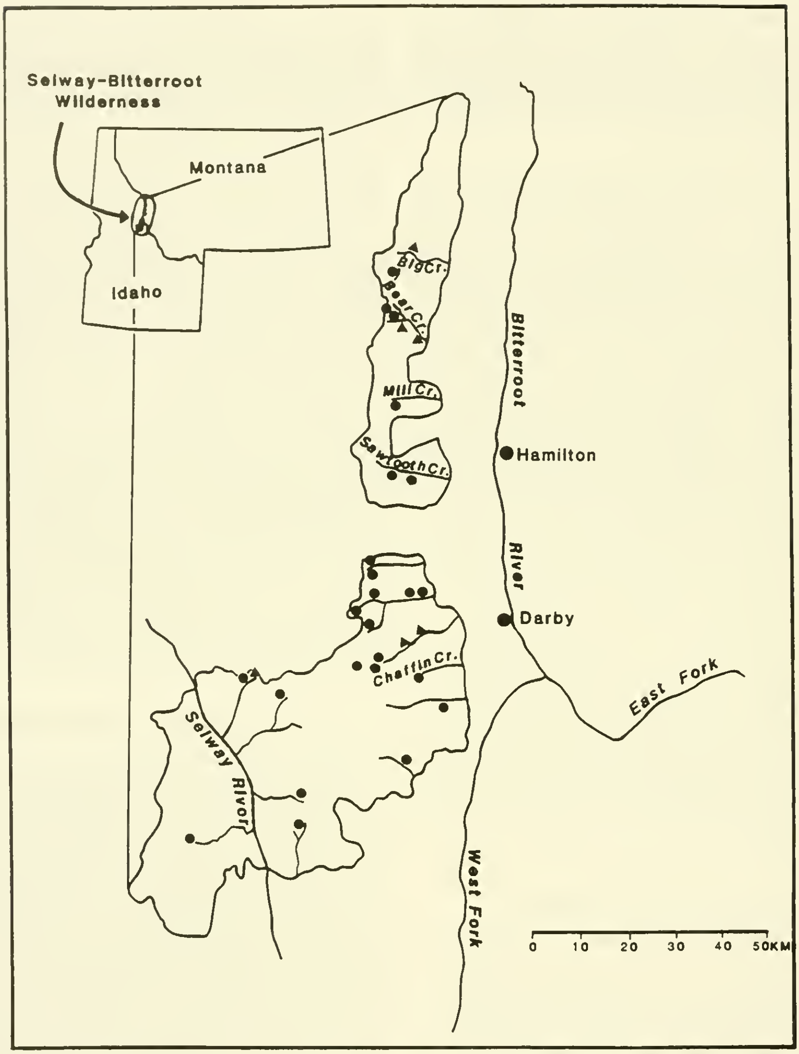
Selway-Bitterroot Wilderness
Montana
Idaho
Big Cr.
Bear Cr.
Mill Cr.
Sawtooth Cr.
Bitterroot
Hamilton
River
Darby
Chaffin Cr.
East Fork
Selway River
West Fork
0 10 20 30 40 50KM

Fig. 1. Spotted knapweed study locations in the Selway-Bitterroot Wilderness Area. Solid circles indicate campsites without spotted knapweed in 1993. Solid triangles are campsites with spotted knapweed. Trails surveyed for spotted knapweed in 1994 parallel Big, Bear, Mill, Sawtooth, and Chaffin creeks. Trailheads of surveyed trails range from 0.0 km to 0.3 km upstream of the wilderness boundary with the exception of Chaffin Creek trailhead, which is 3 km upstream of the wilderness boundary.

area because it receives regular use by hikers and pack stock and because spotted knapweed in non-wilderness portions of the Bitterroot National Forest is common and considered out of control (Losensky 1987). As of 1987 there were 109,600 ha within the forest infested by the plant and another 284,524 ha at risk. Long-distance spotted knapweed dispersal has been associated with contaminated hay (Forcella and Harvey 1983); stock camps in the wilderness therefore may serve as points of weed colonization. There are thus ample seed sources, mechanisms of seed dispersal, and a suitable environment for spotted knapweed to invade the wilderness area.

We surveyed 30 camp sites and 5 trails (Fig. 1), which have elevations ranging from approximately 1400 m to 2400 m. Precipitation in the wilderness area ranges from 1800 mm at 2700 m elevation in higher portions of the northern Bitterroot Mountains to 625 mm in the lower southeastern wilderness at approximately 1200 m elevation (Finklin 1983). Mean monthly temperatures range from −8°C in January to 15°C in July at high elevations and from −2°C in January to 21°C in July at lower sites. Elevations, temperatures, and precipitation in the study area are all well within environmental tolerance levels reported elsewhere for spotted knapweed.

METHODS

We gathered data within stock camps and along trails on spotted knapweed distribution and on environmental and disturbance factors that might affect the species. Environmental information included data on elevations and canopy and vegetation cover. Disturbance data focused on level of disturbance, use by stock or humans, and distances from trailhead and trails. "Stock" camps are used by both hikers and packers. There are no designated backpacker-only camps or trails within the wilderness area.

Thirty camps were surveyed between early June and late August 1993. Four of the camps with spotted knapweed that were along surveyed trails were revisited in 1994. Percent cover of spotted knapweed, bare ground, rocks, litter, moss, grass, forbs, shrubs, and trees was surveyed using a modification of Cole's (1983) method for determining wilderness impact levels. Measurements were taken along 8 equally spaced 24-m transects radiating from the center point of the "human" and "horse" portions of the camp. We differentiated human and horse areas to determine if use type alters spotted knapweed distribution and density. Horse areas were defined on the basis of manure, exposed roots, tree damage from tethers, bare mineral soil, and observations by wilderness rangers. Fire rings, fire scars, and excavated tent pads identified human areas of camps. We used a 2-sample *t* test to test the null hypothesis that there is no significant difference between the number of spotted knapweed plants in human and horse areas of camps. One camp with weeds was eliminated from analysis because horse and human areas could not be clearly separated.

Along each 24-m transect, we located 2 × 2-m quadrats 2 m apart; within each quadrat we counted the number of spotted knapweed plants. To characterize vertical structure of the canopy, we visually estimated vegetation cover variables at 3 heights: ground level to 50 cm, 51 cm to 3 m, and above 3 m. Scatterplot analysis was used to determine the relationship of spotted knapweed to vegetation variables within camp sites where spotted knapweed was present.

Spotted knapweed distribution along 5 trails was surveyed in August and September 1994 (Fig. 1). Starting at the trailhead and recording the distance to trail-side infestations up to 20 m from the trail, we recorded all occurrences of spotted knapweed along each trail. At randomly selected points of infestation along each trail, a transect was established perpendicular to the trail and 1-m^2 quadrats were placed at trail center, 0.5, 1.2, 2.4, 4.6, and 20 m from the trail. In each quadrat the percent canopy cover of spotted knapweed and other species groups (bare ground, moss, grass, herbs, shrubs, and trees) was visually estimated and recorded. Because all sampled trails paralleled streams, we recorded distances from the trail as negative (toward the stream) or positive (away from the stream).

Degree of disturbance in each camp and along trails was initially determined based on "opportunity classes" as defined on existing Forest Service maps. The Selway-Bitterroot is divided into 4 opportunity classes (Selway-Bitterroot Wilderness 1992), which are based on degree of modification of the natural setting and sites, degree of isolation, and frequency of use. A ranking of 1 indicates a pristine, unvisited region, while a ranking of 4 indicates a largely unmodified region but with frequent visitation and locally significant alteration of many of the destination sites.

We also determined disturbance at individual campsites using Selway-Bitterroot Wilderness Site Impacts Worksheets (SIWs), forms used by all wilderness rangers working in the Selway-Bitterroot and by managers throughout the United States. SIWs are modified from worksheets developed by Cole (1989) for documenting wilderness impacts in campsites. The second author of this article (GM) attended the wilderness ranger training session on assessing disturbance with the SIW form and was the only individual to collect SIW data used in this study.

Degree of disturbance at a campsite is assessed based on measures of 8 variables (Table 1). Each variable receives a rating ranging from 1, which is least disturbed, to 3, most

TABLE 1. Variables, ratings, and weighting factors on the Selway-Bitterroot Wilderness Site Impacts Worksheets. Coverage classes for vegetation and mineral soil are class 1: 0–5%; class 2: 6–25%; class 3: 26–50%; class 4: 51–75%; and class 5: 76–100%.

Variable	Definition	Rating 1	Rating 2	Rating 3	Weighting factor
Vegetation loss	Estimated difference between on-site and off-site coverage	no difference in coverage	difference = 1 coverage class	difference >1 coverage class	2
Mineral soil increase	Estimated difference between on-site and off-site coverage	no difference in coverage	difference = 1 coverage class	difference >1 coverage class	3
Tree damage	Total number of damaged trees in the camp site	no more than broken lower branches	1–25 damaged trees or >25% trees damaged	>25 damaged trees or >50% trees damaged	3
Root exposure	Total number of trees with exposed roots caused by erosion or trampling	none	1–15 exposed roots or >25% trees exposed	>15 exposed roots or >50% trees exposed	3
Development	Number and type of facilities found within the camp	no facilities	primitive log or rock seat	facilities other than seat	1
Cleanliness	Amount of trash, fire scars, or manure at the site	no fire scars or rings	1 fire scar/ring, some trash/ manure	>1 fire scar, much trash/ manure or human waste	1
Social trails	Number of trails leading in and out of the camp	no more than 1	2–3 trails, max. 1 well worn	>3 trails, >1 well worn	2
Barren area estimate	Total barren area within the site; considered barren if >90% of the vegetation is absent	<50 ft^2	50–1500 ft^2	>1500 ft^2	3

disturbed. The rating for each variable is multiplied by a weighting factor. Types of impacts that are easily remedied receive a weighting of 1. Impacts that are contained or could recover with less use receive a 2. The heaviest weighting of 3 applies to impacts that are difficult to restore or are long lasting. Weighted rankings are then summed to determine overall campsite impact level, which can fall into 1 of 4 classes: light (18–27), moderate (28–36), heavy (37–45), and extreme (46–54). SIW forms also require noting whether the camp area has a predominantly closed or open canopy. A closed canopy is defined as branches from different trees overlapping over the central campsite. A complete copy of the 4-page SIW is contained in Milner (1995).

Opportunity class and SIW measures generate classes of disturbance ranging from 1 to 3 or 4, depending on the variable in question. Because of the small range of disturbance rank values, a chi-square test was used to statistically evaluate the disturbance hypotheses.

Seed heads were collected from spotted knapweed plants within 3 km of the trailheads along Mill Creek, Big Creek, and Bear Creek trails (Fig. 1). Seed was removed from the seed heads and divided into plump, shriveled, and damaged seeds. Germination of the seed was tested using a standard spotted knapweed protocol (Davis et al. 1993).

RESULTS AND DISCUSSION

Spotted knapweed occurred in 6 of 30 surveyed campsites (Fig. 1, Table 2). Knapweed occurred along very limited portions of all 5 trails, but never beyond 4.6 m from the trail or 7.6 km from the trailhead, with over 95% observed within 0.5 km of the trailhead (Fig. 2, Table 3). More complete summaries of the vegetation transect and SIW disturbance data for each campsite are contained in Milner (1995).

Elevation

All 6 camps containing spotted knapweed are located at <1700 m, which is consistent with Chicoine et al.'s (1985) work in Montana showing 90% of infestation sites occurring at <1829 m (6000 ft; Table 2). There was no spotted knapweed in any camps or along any trails above 1700 m, nor in 10 of the 16 camps below 1700 m.

TABLE 2. Summary characteristics of campsites surveyed for spotted knapweed in the Selway-Bitterroot Wilderness Area. SIW variables and rating scale are described in Table 1.

Elevation (m)	Distance from trailhead (km)	Forest cover		Overall impact		Development		Mineral soil		Vegetation loss		Opportunity class		Average knapweed density (plants/m^2)
		# sites	Cover type	# sites	SIW rating	# sites	SIW rating	# sites	SIW rating	# sites	SIW rating	# sites	Ranking	
6 camps with spotted knapweed														
Avg: 1519	Avg: 9.0	6	open	1	extreme	4	3	4	2	4	2	5	4	Avg: 0.164
Min: 1536	Min: 1.8	0	closed	3	heavy	2	2	2	1	2	1	1	3	Min: 0.012
Max: 1658	Max: 13.3			2	moderate									Max: 0.575
24 camps without spotted knapweed														
Avg: 1858	Avg: 11.5	10	open	10	extreme	15	3	10	3	10	3	5	4	No plants
Min: 1402	Min: 4.4	14	closed	7	heavy	2	2	8	2	7	2	7	3	
Max: 2304	Max: 21.3			7	moderate	7	1	6	1	7	1	9	1	
												3	1	

TABLE 3. Occurrence of spotted knapweed along trails in the Bitterroot portion of the Selway-Bitterroot Wilderness Area.

Trail name	Opportunity class ranking	Distance to final knapweed location (km)	Spotted knapweed per infested trail distance (knapweed/km)
Mill Creek	3 or 4	6.4	2.8
Big Creek	4	7.6	0.3
Chaffin Creek	3	5.3	0.2
Bear Creek (North Fork)	4	1.3	3.8
Sawtooth Creek	2	6.1	0.5

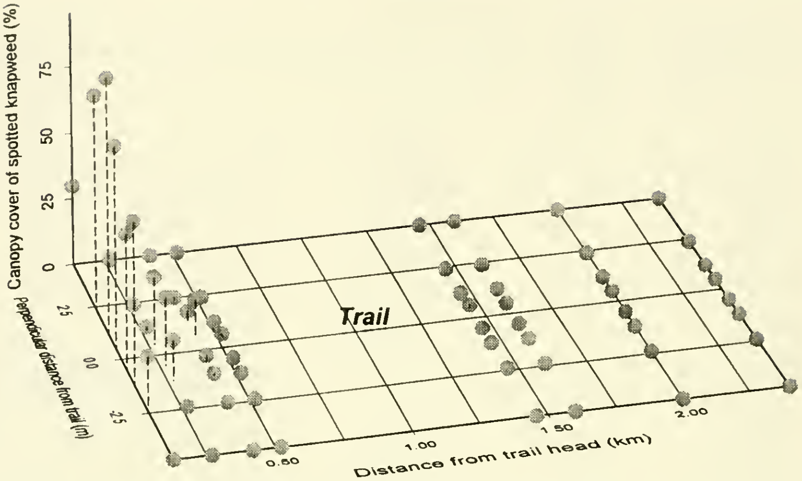

Fig. 2. Percent cover of spotted knapweed relative to distance from trailhead (km) and perpendicular distance (m) to Mill Creek trail. Negative distance indicates distances on the stream side of the trail. Positive distances are on the upslope side of the trail.

Canopy

Spotted knapweed was present in 6 of 10 open canopy camps below 1700 m, but not in any of the 14 closed canopy sites, which included 10 sites below 1700 m (Table 2). A chi-square test indicated a significant relationship at the 0.10 level between open canopy and presence of spotted knapweed in camps (Table 4). Visual observations along trails also suggested that spotted knapweed was more associated with open areas and talus slopes in particular.

Open canopy can result from natural variability in forest cover but can also reflect disturbance such as trampling and cutting down of trees for firewood, ease of movement, and facilities (e.g., hitches). Association of spotted knapweed with open canopy is consistent with work by Watson and Renney (1974), who found it to be more commonly associated with open areas and rarely in shade. Losensky (1987) noted that spotted knapweed germinates equally well under a 0–100% canopy, but shade severely limits growth.

Disturbance and Spotted Knapweed

OPPORTUNITY CLASS AND CAMPSITE INFESTATION.—Five of 10 opportunity class 4 camps and 1 of 8 class 3 campsites contained spotted knapweed (Table 2). No infestations occurred in 12 camps with ratings of opportunity class 1 or 2, which designate areas receiving less use. A chi-square test indicated a significant positive relationship between opportunity class rank and spotted knapweed presence in campsites at the 0.10 level (Table 4). The positive association of opportunity class and spotted knapweed fits with previous research showing that disturbance plays a key role in facilitating spotted knapweed infestation (Watson and Renney 1974, Morris and Bedunah 1984, Mooers 1986, Losensky 1987).

SITE IMPACT RATING AND CAMPSITE INFESTATION.—Unlike the clear association of opportunity class and spotted knapweed, the overall SIW rating for campsites (moderate, heavy, extreme) did not have a significant relationship to presence or absence of spotted knapweed in the Selway-Bitterroot Wilderness (Table 4). This is probably because the overall SIW rating gives significant weighting to a number of variables such as cleanliness, root exposure, and tree damage which, based on existing literature, would not be expected to have a direct connection to spotted knapweed presence or absence. In contrast, opportunity classes are largely defined based on frequency of use and probably provide a better indicator of total numbers of users and the resultant disturbance and potential for seed introduction.

Some components of disturbance that are measured to determine the overall SIW rating do, however, appear to be associated with

TABLE 4. Chi-square test of the relationship between number of spotted knapweed at each campsite ($n = 30$) and possible driving variables. Relationships significant at the 0.10 level are in **boldface.**

Variable	Chi-square	P value
Opportunity class	**8.90**	**0.019**
Variables on SIW sheet		
Vegetation loss	4.36	0.113
Mineral soil	3.96	0.138
Tree damage	0.17	0.680
Root exposure	1.29	0.256
Development	**5.83**	**0.054**
Cleanliness	3.40	0.183
Social trails	1.96	0.375
Barren core area	1.09	0.581
Closed/open forest canopy	**5.64**	**0.010**
Overall SIW impact rating	1.47	0.537

spotted knapweed. Although not significant at the 0.10 level, vegetation loss and mineral soil variables both show weak associations with the presence of spotted knapweed in camps (Table 4). This suggested link between vegetation loss, mineral soil, and presence of spotted knapweed is consistent with previous research indicating that exposed mineral soil provides a fertile area for spotted knapweed germination (Morris and Bedunah 1984, Mooers 1986).

The apparent association of the development variable with spotted knapweed (Table 4) is perplexing. Development as defined on the SIW is the number and type of facilities (e.g., tent poles, log seats, hitch rails, etc.). Four of 19 camps with a development rating of 3 (the most developed) and 2 of 4 that rated a 2 contained spotted knapweed (Table 2). None of the 7 camps with a development rating of 1 contained the weed.

The apparent preference of spotted knapweed for development rating 2 sites may simply reflect the elevations of camps with open canopy rather than a preference for sites with intermediate levels of development. Three of 4 development rating 2 camps are situated below the 1700 m maximum elevation at which spotted knapweed was found in this study, while only 5 of 19 development rating 3 sites are located below 1700 m. Approximately equal proportions of development rating 2 and 3 camps below 1700 m thus contain spotted knapweed. None of the development rating 1 camps contain spotted knapweed, but all are located above 1700 m. Greater development is also associated with open canopy because trees are felled to make hitches, tent poles, seats, and other facilities.

DISTURBANCE AND INFESTATION ALONG TRAILS.—Spotted knapweed occurrence along trails is limited in extent, generally occurring in low-elevation, most frequently visited portions of trails within 0.5 km of trailheads (Fig. 2). Disturbance as indicated by opportunity class ranking also is associated with infestation, with the large majority of weeds growing along the opportunity class 3 and 4 trail sites (Table 3). Spotted knapweed occurred at only 3 open scree sites along the opportunity class 2 Sawtooth Creek trail.

In general, spotted knapweed is most commonly observed along all trails on scree slopes where soil is shallow and rock is often moving over and disturbing the surface. Spotted knapweed cover decreases with distance from the trail (Fig. 2), which may be the result of decreased disturbance associated with activity on the trail or increased distance from sources (people and animals) traveling along the trail. There is also a decrease in knapweed frequency and cover with increased distance from trailheads (Fig. 2). These results are similar to those described by Dale and Weaver (1974).

Stock and Human Use Areas in Camps

In the horse areas of the remaining 5 camps, 16 of 1355 quadrats contained a total of 84 spotted knapweed. In human areas, 13 of 1264 quadrats contained 51 total plants. At the scale of individual campsites, our data indicate no significant difference in spotted knapweed frequency between horse and human areas.

Vegetation in Camps

A Pearson correlation of vegetation cover and spotted knapweed abundance was conducted to determine if local scale variations in ground cover affect the ability of spotted knapweed to colonize. We limited our analysis to the 16 camps below 1700 m where spotted knapweed was known to be viable. The correlation supports the general observation that canopy is key in controlling spotted knapweed (Table 5). The only correlation that was significant at the 0.05 level was the negative correlation ($r = 0.08$) between tree cover above 3 m in height and spotted knapweed density.

TABLE 5. Pearson correlation coefficients (r) for cover categories (%) versus spotted knapweed stem density (stems m^{-2}) in the 16 camps below 1700 m elevation.

Cover variable	r
Bare ground	0.0077
Litter	–0.0357
Moss	0.0164
Forbs	0.0121
Grass	–0.0181
Brush (≤3.0 m)	0.0178
Trees (≤3.0 m)	–0.0377
Brush (>3.0 m)	–0.0160
Trees (>3.0 m)	**–0.0802***

*Significant correlation ($p \le 0.05$)

In 6 camps where spotted knapweed was present and where cover could influence the within-camp distribution, scatterplot analysis indicated that spotted knapweed does best in areas with <25% cover of rock, which simply reflects the inability of the plant to grow without soil. In general, spotted knapweed was present only in quadrats where percent cover of litter, moss, grass, and trees was each <25%, or the total canopy cover was <100% (canopy cover often exceeded 100% because it was measured in 3 different levels and then summed). This is consistent with Morris and Bedunah's (1984) and Mooers' (1986) findings that bare soil enhances the ability of spotted knapweed to invade a site. Percent cover of forbs showed no clear relationship to spotted knapweed.

Spotted knapweed, however, was usually present only in quadrats with <25% bare ground. This partially results because spotted knapweed covers the soil and reduces the percent cover of bare ground. In addition, many areas with significant bare ground in campsites are locations where fire rings, tent sites, and horse hitches are concentrated. While some bare ground is beneficial to spotted knapweed, areas that receive repeated disturbance and soil compaction can make it difficult for any new plant, including spotted knapweed, to become established.

Seed and Plant Viability

In 1994 no knapweed was observed in 3 of 4 camps that were infested in 1993. This suggests that spotted knapweed may be ephemeral in the wilderness and present only under ideal growing conditions.

In plants sampled along Mill, Big, and Bear Creek trails, there was a mean of 16 (±12) seeds per head. This is substantially lower than the 1000 seeds per head generally reported. The proportion of plump seeds ranged from 2% to 100% of seeds in individual heads. No shriveled or damaged seeds germinated, but 100% of plump seeds did. Thus, one may conclude that viable seed is produced in the wilderness but reproductive potential is low.

MANAGEMENT IMPLICATIONS

It is notable that only 6 of 30 wilderness campsites and very small portions of 5 wilderness trails contained spotted knapweed in an area perceived to be at great risk from infestation. Furthermore, spotted knapweed occurred in only 1 of 4 camps infested in 1993 that were revisited the following summer, and seed production was low for specimens collected along the trail during the summer of 1994. If the Bitterroot portion of the Selway-Bitterroot Wilderness is representative of forested wilderness areas in the Northern Rockies, then the perceived threat may substantially exceed the actual danger in many instances. The results from this study suggest 4 general avenues of management responses.

(1) Managers should conduct surveys before initiating costly control measures in any wilderness area. Surveys in forested regions similar to the Selway-Bitterroot should initially focus on areas most prone to infestation, that is, areas with open canopy adjacent to trails where opportunity class ratings are 3 or greater and in elevations that are optimal for spotted knapweed.

(2) Wilderness workers can be trained to remove weeds as part of their normal backcountry duties. Likewise, volunteers can be educated and recruited to remove weeds via existing weed awareness programs, signing of trails, and information packets given to backcountry users.

(3) The association of spotted knapweed at campsites with loss of vegetation, exposed mineral soil, open canopy, and development of facilities emphasizes the need for already existing regulations promoting minimum-impact camping in wilderness areas. In particular, backcountry permits should stress packing in camp chairs and using aluminum poles for tent poles and hitches rather than tearing down dead wood or cutting live trees, both of which open up the canopy.

(4) The tendency for spotted knapweed to grow only on scree slopes along trails suggests that infestation could be avoided by routing trails to avoid these open disturbed areas.

This research leaves open the question of how serious the spotted knapweed problem is in surrounding forested, non-wilderness portions of the Bitterroot National Forest and whether the same variables of elevation, open canopy, and opportunity class can be used to predict potential for infestation on those lands. There is clearly a vast gulf between the perception of infestation and the reality in some areas. This uncertainty suggests that, at a minimum, further surveys should be conducted in different use areas to determine where the threat is serious, what variables control that threat, and how to best allocate resources to control spotted knapweed.

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BREEDING BIRDS AT THE IDAHO NATIONAL ENGINEERING AND ENVIRONMENTAL LABORATORY, 1985–1991

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ABSTRACT.—During the summers of 1985–1991, bird censuses were conducted along 13 permanent routes located at the 2315-km^2 Idaho National Engineering and Environmental Laboratory (INEEL, formerly INEL) in southeastern Idaho. The objectives of the surveys were to (1) compare avifauna in and near facility complex sites with remote, relatively undisturbed habitats, (2) identify trends in populations of sagebrush-obligate species and other common shrubsteppe species, and (3) determine the presence, abundance, and population status of species of special concern. Five routes were official U.S. Geological Survey, Biological Resources Division 40.0-km Breeding Bird Survey (BBS) routes (formerly administered by the U.S. Fish and Wildlife Service) located in relatively remote portions of the INEEL where access by humans was controlled and limited. Eight shorter routes (5.8–19.2 km in length) were near INEEL facility complexes, which more regularly experienced disturbance by humans. The surveys recorded 25,597 individuals representing 90 species. Western Meadowlarks (*Sturnella neglecta*), Brewer's Sparrows (*Spizella breweri*), Sage Sparrows (*Amphispiza belli*), Horned Larks (*Eremophila alpestris*), and Sage Thrashers (*Oreoscoptes montanus*) comprised 72% of all individuals. Almost half of all species were represented by fewer than 10 individuals. Bird density was significantly greater along facility complex routes. Moreover, because of human-constructed wetlands and structures of various types, facility complex routes had significantly more bird species per unit area, including more species of waterfowl and human-associated species. Some year-to-year variation in bird density was related to weather. More individuals were recorded in cooler, wetter years, although such increases were reflected more along facility complex routes. Among sagebrush-obligate species, trend analysis suggests that both Brewer's Sparrows and Sage Sparrows increased significantly in abundance, which may be in contrast to regional trends for these species. Of 5 species of special concern observed, trend analysis could be performed for only 2: Ferruginous Hawks (*Buteo regalis*) and Loggerhead Shrikes (*Lanius ludovicianus*). Both species had more routes with negative regression coefficients and negative trend means, indicating that declines may have occurred, although the goodness-of-fit test for neither species was significant. These data from the INEEL should be useful for comparison with future studies at the site and other studies from throughout the Great Basin region.

Key words: Idaho National Engineering and Environmental Laboratory (INEEL), avifauna, sagebrush shrubsteppe, sagebrush obligates.

Although a number of recent reports document population changes in the avifauna of the eastern or midwestern U.S. (e.g., Askins et al. 1990, Sauer and Droege 1990, 1992, Hagan and Johnston 1992, Finch and Stangel 1993, Hagan 1993, Peterjohn and Sauer 1994, Hekert 1995), patterns of population change in western bird species have remained largely understudied. Dobkin (1994) noted that fewer studies in the West may be a result of fewer Breeding Bird Survey routes and proportionately greater non-urban/suburban habitat compared to the eastern U.S. Additionally, insufficient route coverage over much of the western U.S. has limited attempts to compare trends between periods in BBS data for populations of many western species (e.g., see Sauer and Droege 1992). Despite such limitations, Paige (1990) indicated there are key species in every major habitat in the West that warrant either concern or immediate action. Of particular interest in her analysis were shrubsteppe and grassland habitats, which apparently experienced widespread declines in avifauna between 1966 and 1985 (Paige 1990). Additional and more recent information concerning avian populations in shrubsteppe and grassland habitats would be useful to determine whether such declines have continued or have been exacerbated.

The Idaho National Engineering and Environmental Laboratory (INEEL), located in southeastern Idaho, is a federal facility containing large expanses of shrubsteppe habitat within its boundaries. In contrast to many other sites in southern Idaho and elsewhere where this habitat type has been converted for crop and hay production, or severely altered by invasion of exotic species of annuals, shrubsteppe habitat at the INEEL remains relatively undisturbed because there are few roads, access by humans to much of the area is controlled and limited, and there is no crop or hay production. Instead, this area was designated as a National Environmental Research Park in 1975 and serves as an outdoor laboratory to assess impacts of energy development technologies on the environment. Although the vertebrate fauna on the area have been described (Reynolds et al. 1986), little information exists concerning how the avifauna changes with time, or how changing land-use patterns and other activities affect the structure or abundance of avian populations. Therefore, because of the paucity of information on population status of breeding birds in the western U.S., and because the INEEL provides an ideal study site for conducting longer-term studies within shrubsteppe habitat, we examined the avifauna by censusing permanent survey routes for birds each summer.

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Specifically, our objectives in the present study were to (1) identify bird species present at the INEEL during the summer breeding season; (2) assess the effects of INEEL activities by comparing the abundance and composition of avifauna occupying facility complex sites and more remote habitats; (3) identify trends in abundance of sagebrush-obligate species (i.e., species characteristic of the shrubsteppe habitat that require large areas of unfragmented sagebrush habitat) and other common shrubsteppe species; (4) determine the presence, abundance, and population status of species of special concern in Idaho; and finally (5) generate baseline information concerning populations of breeding birds at the INEEL, which hopefully will be useful for comparisons with ongoing and future studies both at the site and in shrubsteppe habitat throughout the western U.S.

STUDY AREA

The 2315-km^2 INEEL is located approximately 48 km west of Idaho Falls, on the upper Snake River Plain in portions of Bonneville, Butte, Bingham, Jefferson, and Clark counties, Idaho. The area is dominated by semiarid, cold desert shrubland with an average elevation of approximately 1500 m above sea level. The climate, geology, and vegetation of this high desert area are described in detail by Anderson and Holte (1981) and Anderson et al. (1996). Briefly, vegetation at the site is characteristic of shrubsteppe habitat and dominated by woody, mid-height shrubs and perennial bunchgrasses. Common plant species include sagebrush (*Artemisia* spp.), rabbitbrush (*Chrysothamnus viscidiflorus*), shadscale (*Atriplex confertifolia*), winterfat (*Krascheninnikovia lanata*), squirreltail (*Elymus elymoides*), thickspike wheatgrass (*Elymus lanceolatus*), needle and thread grass (*Hesperostipa comata*), and ricegrass (*Achnatherum hymenoides*). In general, the topography is flat to gently rolling, with lava outcroppings characteristic of the Columbia Plateau Province. The area experiences hot summers, cold winters, frequent wind, and low soil stability (Short 1986). Annual precipitation, averaging approximately 20 cm/ yr, is produced mainly during spring rain and snow events. Surface water is limited to residual flows of the Big Lost Rivers and Birch Creek, each of which is diverted upstream for agriculture and flood prevention, and several (0.3–15.8 ha in size) human-constructed ponds near research facilities. Grazing by sheep and cattle occurs but is seasonal and concentrated on the periphery of INEEL where the site borders Bureau of Land Management (BLM) and private holdings. Stocking densities in areas grazed at INEEL are lower (10 ac/AUM) than those on neighboring BLM lands (6 ac/AUM).

METHODS

Survey Routes and Procedures

Thirteen permanent avian census routes were established within the study area (Fig. 1). These include 40.0-km routes (n = 5 standard Breeding Bird Survey [BBS] routes administered by U.S. Geological Survey, Biological Resources Division) that traverse the major habitat types within more remote regions of the site (Table 1, Fig. 1). For brevity, hereafter we refer to these as *remote routes*, and the areas in which they are located as *remote areas*. Eight shorter routes, averaging 8.5 km in length, are around major INEEL facility complexes (Table 1), where effects of site activities on the abundance and composition of avifauna are assessed in comparison to remote areas. We refer to these routes as *facility complex routes*. The 13 routes were surveyed for

TABLE 1. Summary of length of route, number of stops, and area surveyed along permanent bird survey routes ($n = 5$ remote routes, $n = 8$ facility complex routes) at the Idaho National Environmental and Engineering Laboratory in southeastern Idaho. Major habitat associations along each route and mean (± *s*) number of species and individuals (number/km²) observed along each route, 1985–1991, also are summarized.

Route	Length (km)	No. stops	Area (km²)	No. species	No. individuals	Major habitat types[a] (percentage of route)
REMOTE ROUTES						
Twin Buttes (TB)	10.0	50	25.1	17.3 ± 1.9	12.9 ± 3.4	1 (16), 2 (31), 8 (16), 9 (12), 11 (17), 13 (4), 15 (4)
Lost River (LR)	40.0	50	25.1	15.8 ± 1.3	12.3 ± 3.4	1 (76), 3 (12), 12 (12)
Kyle Canyon (KC)	40.0	50	25.1	22.8 ± 3.9	11.7 ± 2.7	3 (20), 4 (20), 6 (10), 7 (12), 11 (16), 12 (14), 14 (8)
Circular Butte (CB)	40.0	50	25.1	13.0 ± 1.5	13.0 ± 5.5	2 (4), 3 (6), 5 (60), 10 (20), 12 (10)
Tractor Flats (TF)	40.0	50	25.1	17.3 ± 2.3	18.9 ± 6.1	1 (8), 2 (23), 8 (7), 10 (40), 13 (22)
FACILITY COMPLEX ROUTES						
Idaho Chemical Processing Plant (ICPP)	8.0	25	2.01	13.4 ± 1.8	88.0 ± 30.6	3 (100)
Test Reactor Area (TRA)	10.2	32	2.57	13.4 ± 3.6	102.2 ± 60.1	3 (100)
Central Facilities Area (CFA)	9.6	42[b]	3.38	18.6 ± 1.5	88.3 ± 19.4	2 (75), 3 (25)
Naval Reactors Facility (NRF)	6.4	20	1.61	22.4 ± 5.4	168.7 ± 57.4	2 (100)
Test Area North (TAN)	19.2	60	4.82	18.1 ± 4.0	92.2 ± 40.6	4 (40), 10 (15), 14 (45)
Power Burst Facility (PBF)	9.0	28[c]	2.25	12.1 ± 1.9	81.1 ± 28.3	2 (80), 13 (20)
Radioactive Waste Management Complex (RWMC)	5.8	18	1.45	12.7 ± 2.4	72.3 ± 11.1	1 (100)
Argonne National Laboratory–West (ANL-W)	5.8	18	1.45	20.1 ± 3.5	136.9 ± 27.8	2 (80), 15 (20)

[a] Habitat types: (1) *Artemisia tridentata–Pseudoroegneria spicata–Chrysothamnus viscidiflorus*, (2) *Artemisia tridentata–Chrysothamnus viscidiflorus–Elymus elymoides*, (3) *Artemisia tridentata–Elymus lanceolatus–Hesperostipa comata*, (4) *Artemisia tridentata–Krascheninnikovia lanata–Chrysothamnus viscidiflorus*, (5) *Artemisia tridentata–Achnatherum hymenoides–Hesperostipa comata*, (6) *Artemisia tridentata–Krascheninnikovia lanata–Atriplex confertifolia*, (7) *Artemisia arbuscula–Artemisia tridentata–Atriplex confertifolia*, (8) *Agropyron cristatum* (seeded), (9) *Pseudoroegneria spicata–Artemisia tripartita–Chrysothamnus viscidiflorus*, (10) *Achnatherum hymenoides–Chrysothamnus viscidiflorus–Opuntia polyacantha*, (11) *Juniperus osteosperma–Artemisia tridentata–Pseudoroegneria spicata*, (12) *Tetradymia canescens–Chrysothamnus viscidiflorus–Artemisia tridentata*, (13) *Chrysothamnus viscidiflorus–Artemisia tridentata*, (14) *Atriplex nuttalii–Krascheninnikovia lanata–Achnatherum hymenoides*, (15) *Leymus cinereus–Chrysothamnus viscidiflorus–Pseudoroegneria spicata*.

[b] Only 30 stops were included in 1985.

[c] Thirty stops made in 1986.

birds in June of each year between 1985 and 1991, with the exception of 4 individual route surveys (3 in 1985, 1 in 1990), which were performed in early July because of delays caused by unsuitable weather. Beginning 0.5 h before sunrise, we recorded the number of individuals of each bird species seen or heard during 3-min observation sessions at each stop along the route. For remote routes, we located stops every 0.8 km and counted birds if they occurred within 0.4 km of the stop. Surveys along the shorter facility complex routes were performed in a similar fashion, except that stops were 0.32 km apart and birds were recorded only if they were within 0.16 km (i.e., half the distance between stops) of the observer. Stops were visited in the same order each year, but surveys were conducted only when weather conditions were considered satisfactory according to BBS guidelines.

Finally, 4 different observers performed the surveys. Because 3 observers each performed the surveys for 2 consecutive years (1985–86, 1987–88, 1990–91), and the 4th conducted surveys in only 1 yr (1989), the possibility of interobserver (Sauer et al. 1994) and 1st-time observer (Kendall et al. 1996) effects in the data set cannot be ruled out. For example, Kendall et al. (1996) noted that trend estimates for many species based on formal breeding bird survey route data decreased by an average of 1.8% per year when data from an observer's 1st yr were excluded, and the authors suggested the difference was most likely a result of observers' improvements in counting birds in subsequent years. Kendall et al. (1996) suggested that to reduce 1st-time observer effects, 1st-yr data could be eliminated from analyses, or the effects might be reduced by improved training of observers prior to their 1st survey. Because our study was of relatively short duration in comparison to the Breeding Bird Survey, which has been underway since the mid-1960s (Robbins et al. 1986, 1989), we are unable to eliminate

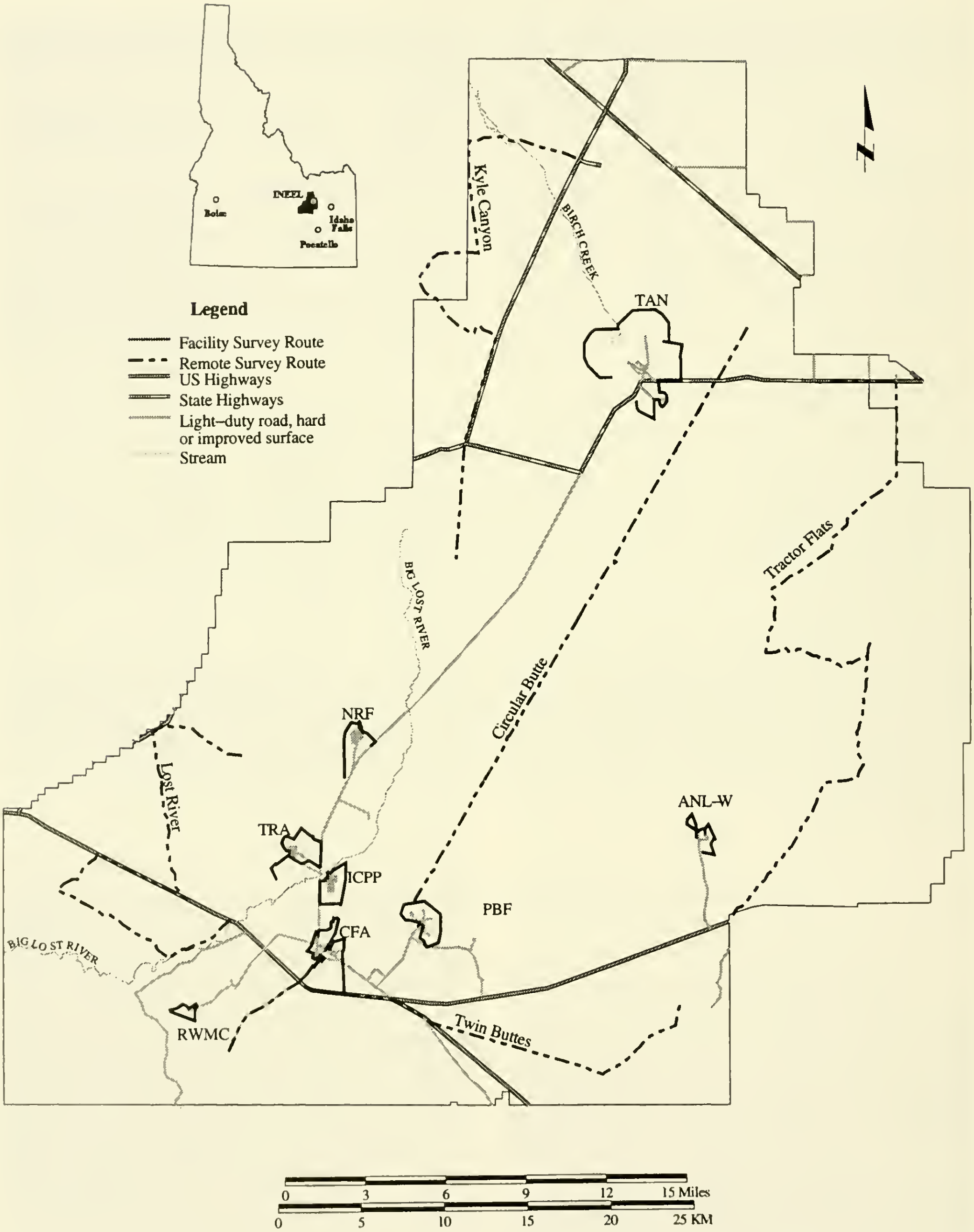
Boise
INEEL
Idaho Falls
Pocatello
Legend
Facility Survey Route
Remote Survey Route
US Highways
State Highways
Light–duty road, hard or improved surface
Stream
Kyle Canyon
BIRCH CREEK
TAN
BIG LOST RIVER
Tractor Flats
Circular Butte
NRF
Lost River
TRA
ICPP
ANL-W
PBF
CFA
BIG LOST RIVER
RWMC
Twin Buttes
0 3 6 9 12 15 Miles
0 5 10 15 20 25 KM

Fig. 1. Relative locations of remote routes and facility complex routes for breeding bird census at the INEEL, 1985–1991. Route designators relate to those in Table 1.

the 4 yr of data in which 1st-time observers performed the surveys; instead, we made every effort to reduce potential interobserver and 1st-time observer effects using the latter recommendation of Kendall et al. (1996). In our study all survey personnel were skilled with bird identification in the habitats of interest, they typically had experience in performing standardized surveys for birds, and they were routinely trained in the point-count method prior to beginning the surveys.

Data Analyses

Each year, and for each route, we recorded number of birds observed and number of species detected (species richness). Because the radius of surveys around stops was not equal between types of routes, we also transformed bird abundance and species data to per-unit-area (km^2) measures to allow more appropriate comparisons between types of routes. Then, to assess differences in bird abundance and species richness between types of routes and among years, we performed 2-factor, repeated-measures ANOVAs (Winer et al. 1991) using the Statistical Analysis System (SAS®, Version 6.1, SAS Institute, Cary, NC), with type of route as the between-group factor and year of survey (1985–1991) as the within-subjects or repeated factor. We examined assumptions (e.g., sphericity) for repeated-measures analyses using the REPEATED statement in SAS prior to analysis and used Fisher's protected least significant difference for means comparisons at a rejection level (i.e., α) of 0.05.

We also examined relationships between weather and climate variables and bird abundance and species richness using the nonparametric Spearman's correlation analysis (Sokal and Rohlf 1995, conducted using SAS's CORR procedure). Weather data were from the National Oceanic and Atmospheric Administration monitoring station operated at the Central Facilities Complex, which is located in the southern portion of the study area but relatively centrally among the facility complexes. Although some variation in weather is likely between the survey routes and this station, and among survey routes, these data should provide a general indication of weather conditions at the site during each survey year. For June 1985–1991, which is the month during which most individual surveys were performed, we calculated mean daily maximum temperature (all temperatures are reported as °C), mean daily minimum temperature, mean daily temperature (i.e., daily maximum minus daily minimum and averaged across days of month), maximum monthly temperature, minimum monthly temperature, and total monthly precipitation (cm).

Finally, to examine trends in populations of sagebrush-obligate species, common shrubsteppe species, and species of special concern, using the REG procedure in SAS we regressed against year (1) the total number of individuals per route, and (2) number of individuals per km^2 surveyed for each of the 13 routes (see Atkinson 1995). We included only those routes for which the species of interest was detected in ≥ 5 yr. We subsequently (1) averaged regression coefficients to calculate trend means and (2) determined the number of routes for which regression coefficients were positive and tested the observed distribution against a null random distribution (e.g., that half of the coefficients should be positive) using a χ^2 goodness-of-fit test (including Yates correction for continuity, Zar 1996). We used this approach rather than the route regression approach used in more expanded studies of standardized Breeding Bird Survey data because the majority of routes in our study were not standard BBS routes and the 7 yr of data from our study would result in degrees of freedom below those recommended for the latter (see Geissler and Sauer 1990).

RESULTS

From 1985 through 1991, we recorded 25,597 individuals representing 90 species along 13 survey routes (Tables 1, 2). Western Meadowlarks (*Sturnella neglecta*) were most abundant; this species occurred along all 13 routes and at approximately 62% of the 4991 stops. Other common species were Brewer's Sparrows (*Spizella breweri*), Sage Sparrows (*Amphispiza belli*), Horned Larks (*Eremophila alpestris*), and Sage Thrashers (*Oreoscoptes montanus*), each of which occurred at more than 1100 stops and along all 13 routes (Table 2). These 5 species accounted for approximately 72% of all individuals over the study period. Mourning Doves (*Zenaida macroura*), Brown-headed Cowbirds (*Molothrus ater*), and Common Nighthawks (*Chordeiles minor*) also occurred along each of the 13 routes but in smaller numbers than the preceding species. None of the other 82 species were recorded along all 13 survey routes (Table 2). Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) and Franklin's Gulls (*Larus pipixcan*) also were relatively abundant, but these 2 species were present along fewer routes and

TABLE 2. Species and number of birds observed along bird survey routes (n = 13) at the Idaho National Engineering and Environmental Laboratory, 1985–1991.

		Overall					Annual values	
Common name	Scientific name	No.	%	Routes[b]	Stops[c]	%	No. ($\bar{x} \pm s$)	Stops ($\bar{x} \pm s$)
Western Meadowlark	*Sturnella neglecta*	4497	17.6	5,8	2129	61.9	642 ± 275.6	304 ± 84.4
Brewer's Sparrow	*Spizella breweri*	4297	16.8	5,8	1711	49.7	614 ± 430.3	244 ± 114.9
Sage Sparrow	*Amphispiza belli*	3731	14.6	5,8	1830	53.2	533 ± 297.2	261 ±89.4
Horned Lark	*Eremophila alpestris*	3348	13.1	5,8	1195	34.7	478 ± 123.6	171 ± 36.9
Sage Thrasher	*Oreoscoptes montanus*	2441	9.5	5,8	1670	48.5	349 ± 91.8	239 ± 61.8
Mourning Dove	*Zenaida macroura*	996	3.9	5,8	600	17.4	142 ± 64.4	86 ± 33.0
Brown-headed Cowbird	*Molothrus ater*	875	3.4	5,8	427	12.4	125 ± 59.4	61 ± 20.0
Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	610	2.4	2,4	70	2.0	87 ± 67.5	10 ± 6.0
Franklin's Gull	*Larus pipixcan*	495	1.9	1,4	16	0.5	71 ± 178.4	2 ± 4.4
Common Nighthawk[a]	*Chordeiles minor*	495	1.9	5,8	288	8.4	71 ± 30.6	41 ± 16.2
Brewer's Blackbird	*Euphagus cyanocephalus*	375	1.5	4,8	143	4.2	54 ± 22.9	20 ± 6.9
Killdeer	*Charadrius vociferus*	353	1.4	3,8	173	5.0	50 ± 16.5	25 ± 8.0
Vesper Sparrow	*Pooecetes gramineus*	308	1.2	5,7	151	4.4	44 ± 63.8	22 ± 28.5
Loggerhead Shrike	*Lanius ludovicianus*	280	1.1	5,7	210	6.1	40 ± 18.7	30 ± 10.9
European Starling	*Sturnus vulgaris*	186	0.7	1,8	57	1.7	27 ± 20.0	8 ± 6.6
Wilson's Phalarope	*Steganopus tricolor*	166	0.6	1,2	10	0.3	24 ± 35.4	1 ± 0.5
Black-billed Magpie	*Pica pica*	164	0.6	4,5	110	3.2	23 ± 12.6	16 ± 7.2
Sage Grouse	*Centrocercus urophasianus*	163	0.6	5,5	34	1.0	23 ± 32.0	5 ± 4.6
Barn Swallow[a]	*Hirundo rustica*	152	0.6	2,8	70	2.0	22 ± 8.7	10 ± 3.9
Short-eared Owl	*Asio flammeus*	144	0.6	5,7	91	2.6	21 ± 37.5	13 ± 21.3
Ferruginous Hawk	*Buteo regalis*	95	0.4	5,5	73	2.1	14 ± 3.3	10 ± 2.6
Bank Swallow[a]	*Riparia riparia*	95	0.4	2,2	25	0.7	14 ± 10.8	4 ± 1.3
American Robin	*Turdus migratorius*	84	0.3	4,4	42	1.2	12 ± 6.8	6 ± 3.3
Canada Goose	*Branta canadensis*	82	0.3	1,1	2	0.1	12 ± 26.8	<1
House Sparrow	*Passer domesticus*	79	0.3	0,1	10	0.3	11 ± 16.2	1 ± 0.8
American Kestrel	*Falco sparverius*	72	0.3	4,6	53	1.5	10 ± 5.5	8 ± 4.4
Red-tailed Hawk	*Buteo jamaicensis*	67	0.3	4,7	63	1.8	10 ± 11.3	9 ± 10.2
House Finch	*Carpodacus mexicanus*	67	0.3	0,6	20	0.6	10 ± 9.6	3 ± 1.9
Northern Harrier	*Circus cyaneus*	60	0.2	5,5	54	1.6	9 ± 4.0	8 ± 4.0
Common Raven	*Corvus corax*	57	0.2	5,3	45	1.3	8 ± 5.5	6 ± 3.3
Lark Bunting	*Calamospiza melanocorys*	49	0.2	1,2	17	0.5	7 ± 16.8	2 ± 5.6
Northern Shoveler	*Anas clypeata*	48	0.2	0,2	15	0.4	7 ± 7.0	2 ± 1.4
Lark Sparrow	*Chondestes grammacus*	42	0.2	3,1	23	0.7	6 ± 6.1	3 ± 2.9
Common Flicker	*Colaptes auratus*	40	0.2	3,0	33	1.0	6 ± 3.8	5 ± 2.9
Mallard	*Anas platyrhynchos*	36	0.1	0,2	6	0.2	5 ± 8.4	1 ± 0.9
Ruddy Duck	*Oxyura jamaicensis*	36	0.1	0,2	10	0.3	5 ± 1.8	1 ± 0.5
Cinnamon Teal	*Anas cyanoptera*	33	0.1	0,2	8	0.2	5 ± 6.8	1 ± 1.1
Chipping Sparrow	*Spizella passerina*	33	0.1	1,0	13	0.4	5 ± 4.6	2 ± 2.0
Rock Wren	*Salpinctes obsoletus*	33	0.1	4,5	21	0.6	5 ± 6.7	3 ± 3.6
American Avocet	*Recurvirostra americana*	30	0.1	0,1	4	0.1	4 ± 6.4	1 ± 0.5
N. Rough-winged Swallow	*Stelgidopteryx serripennis*	30	0.1	1,5	16	0.5	4 ± 4.5	2 ± 1.8
Gadwall	*Anas strepera*	28	0.1	0,3	7	0.2	4 ± 6.2	1 ± 1.5
Blue-winged Teal	*Anas discors*	26	0.1	0,2	6	0.2	4 ± 5.4	1 ± 1.5
Swainson's Hawk[a]	*Buteo swainsoni*	23	0.1	5,2	22	0.6	3 ± 1.4	3 ± 1.4
Lazuli Bunting	*Passerina amoena*	23	0.1	1,0	15	0.4	3 ± 5.2	2 ± 3.4
Redhead	*Aythya collaris*	21	0.1	0,2	4	0.1	3 ± 3.2	1 ± 0.5
Rock Dove	*Columba livia*	17	0.1	0,1	5	0.1	2 ± 3.3	1 ± 1.2
American Coot	*Fulica americana*	16	0.1	0,2	9	0.3	2 ± 2.1	1 ± 1.0
Say's Phoebe	*Sayornis saya*	16	0.1	1,6	14	0.4	2 ± 3.0	2 ± 2.9
Gray Flycatcher	*Empidonax wrightii*	14	0.1	2,1	10	0.3	2 ± 2.9	1 ± 2.2
Burrowing Owl	*Athene cunicularia*	13	0.1	4,3	12	0.3	2 ± 3.1	2 ± 3.0
Northern Pintail	*Anas acuta*	9	<0.1	0,1	2	0.1	1 ± 3.0	<1
Prairie Falcon	*Falco mexicanus*	9	<0.1	2,1	8	0.2	1 ± 1.4	1 ± 1.4
Cliff Swallow[a]	*Petrochelidon pyrrhonota*	9	<0.1	1,1	2	0.1	1 ± 2.6	<1
Lesser Scaup	*Aythya affinis*	8	<0.1	0,2	3	0.1	1 ± 1.7	<1
Eastern Kingbird[a]	*Tyrannus tyrannus*	8	<0.1	2,2	5	0.1	1 ± 1.9	1 ± 1.1
Clark's Nutcracker	*Nucifraga columbiana*	8	<0.1	1,0	1	0.0	1 ± 3.0	<1
Red-winged Blackbird	*Agelaius phoeniceus*	7	<0.1	1,2	4	0.1	1 ± 1.5	1 ± 0.8

TABLE 2. Continued.

		Overall					Annual values	
Common name	Scientific name	No.	%	Routes[b]	Stops[c]	%	No. ($\bar{x} \pm s$)	Stops ($\bar{x} \pm s$)
Violet-green Swallow	*Tachycineta thalassina*	7	<0.1	2,2	5	0.1	1 ± 1.8	1 ± 1.1
Ring-billed Gull	*Larus delawarensis*	6	<0.1	2,2	4	0.1	1 ± 0.9	1 ± 0.8
Common Goldeneye	*Bucephala clangula*	6	<0.1	1,1	2	0.1	1 ± 1.9	<1
Great Horned Owl	*Bubo virginianus*	6	<0.1	1,2	3	0.1	1 ± 1.5	<1
Western Kingbird[a]	*Tyrannus verticalis*	6	<0.1	2,1	5	0.1	1 ± 0.9	1 ± 0.8
Ring-necked Pheasant	*Phasianus colchicus*	6	<0.1	0,3	5	0.1	1 ± 1.5	1 ± 1.1
Willet	*Catoptrophorus semipalmatus*	5	<0.1	1,1	5	0.1	1 ± 0.8	1 ± 0.8
Common Poor-will	*Phalaenoptilus nuttalii*	5	<0.1	1,0	4	0.1	1 ± 1.9	1 ± 1.5
Spotted Sandpiper	*Actitis macularia*	4	<0.1	0,2	3	0.1	1 ± 0.8	<1
Mountain Bluebird	*Sialia currucoides*	4	<0.1	1,0	3	0.1	1 ± 1.0	<1
Gray Partridge	*Perdix perdix*	4	<0.1	3,0	3	0.1	1 ± 1.1	<1
California Gull	*Larus californicus*	3	<0.1	2,0	3	0.1	<1	<1
Caspian Tern	*Sterna caspia*	3	<0.1	1,0	1	<0.1	<1	<1
Forster's Tern	*Sterna forsteri*	3	<0.1	1,0	1	<0.1	<1	<1
Long-billed Curlew	*Numenius americanus*	3	<0.1	1,0	2	0.1	<1	<1
Golden Eagle	*Aquila chrysaetos*	3	<0.1	1,1	3	0.1	<1	<1
Blue Gray Gnatcatcher	*Polioptila caerulea*	3	<0.1	1,0	2	0.1	<1	<1
Green-winged teal	*Anas crecca*	2	<0.1	0,1	1	<0.1	<1	<1
Wood Duck	*Aix sponsa*	2	<0.1	0,1	1	<0.1	<1	<1
White-faced Ibis	*Plegadis chihi*	2	<0.1	1,0	1	<0.1	<1	<1
Cooper's Hawk	*Accipiter cooperii*	2	<0.1	1,0	2	0.1	<1	<1
Savannah Sparrow	*Passerculus sandwichensis*	2	<0.1	0,1	2	0.1	<1	<1
Green-tailed Towhee	*Pipilo chlorurus*	2	<0.1	1,0	2	0.1	<1	<1
Eared Grebe	*Podiceps nigricollis*	1	<0.1	1,0	1	<0.1	<1	<1
Sora	*Porzana carolina*	1	<0.1	0,1	1	<0.1	<1	<1
Greater Yellowlegs	*Tringa melanoleuca*	1	<0.1	0,1	1	<0.1	<1	<1
Merlin	*Falco columbarius*	1	<0.1	1,0	1	<0.1	<1	<1
Willow Flycatcher[a]	*Empidonax traillii*	1	<0.1	0,1	1	<0.1	<1	<1
American Crow	*Corvus brachyrhynchos*	1	<0.1	1,0	1	<0.1	<1	<1
Orchard Oriole[a]	*Icterus spurius*	1	<0.1	1,0	1	<0.1	<1	<1
Song Sparrow	*Melospiza melodia*	1	<0.1	1,0	1	<0.1	<1	<1
Mountain Chickadee	*Poecile gambeli*	1	<0.1	1,0	1	<0.1	<1	<1
TOTAL		25,597	100.0					

[a] Winters exclusively south of the U.S. (after Dobkin 1994).

[b] Number of remote routes along which species occurred, number of facility complex routes along which species occurred.

[c] Number of stops at which species was detected, total stops surveyed = 4991.

occurred at very few stops along those routes (Table 2). Many species observed within the study area were neither widespread nor abundant. For example, 28 species (31.1%) occurred along only 1 of the 13 routes, and 39 species (43.3%) were represented by fewer than 10 individuals (Table 2).

Comparisons Between Types of Routes

There were no significant differences between remote routes and facility complex routes for the absolute number of individuals or species (richness) observed (Table 3). However, both average number of birds per km^2 surveyed and average number of species per km^2 were significantly greater for facility complex routes (Table 3). Thus, despite the fact that these routes were shorter in length than remote routes and that a smaller diameter around each stop was censused, there were more individuals and more species per unit area along facility complex routes.

Species Assemblages

In addition to differences in density of individuals and the number of species per km^2, the composition of species also differed between remote routes and facility complex routes.

WATERFOWL.—Of the 14 species of waterfowl (order Anseriformes, family Anatidae) detected along the survey routes (Table 2), only 2 species (14%) were recorded along remote

TABLE 3. Comparison of bird survey results between routes located near INEEL facility complex sites ($n = 8$) and those in remote areas ($n = 5$). Means ($\pm s_{\bar{x}}$) of dependent variables and results of 2-factor repeated-measures ANOVA are presented. Note: Year was a repeated factor in the analysis.

Variable	Facility complex routes ($\bar{x} \pm s_{\bar{x}}$)	Remote routes ($\bar{x} \pm s_{\bar{x}}$)	$F_{1,11}$	P
Birds recorded	240.6 ± 32.8	346.3 ± 41.4	4.0	0.071
Avg. number of birds/km^{2a}	103.7 ± 9.2	13.8 ± 11.7	47.1	<0.001
Species richness	16.4 ± 1.3	17.3 ± 1.7	0.2	0.692
Avg. number of species/km^2	7.9 ± 1.1	0.7 ± 1.4	16.2	0.002

[a]Significant interaction between type of route and year for this variable; see Figure 3.

routes: Canada Goose (*Branta canadensis*) and Common Goldeneye (*Bucephala clangula*).

SHOREBIRDS, GULLS, AND WADERS.—Thirteen species of shorebirds/wading birds/gulls and terns were observed (Table 2). Of these, 5 were observed along remote routes only, 3 species were observed along facility complex routes only, and the remaining 5 occurred along both types of route. The most abundant species among these was Franklin's Gull, which was observed along 4 of 8 facility complex routes but only 1 remote route (Table 2).

RAPTORS.—Twelve species of raptors, including eagles, falcons, hawks, and owls, were observed along the survey routes. Although most species of raptors were detected equally along both types of routes, Swainson's Hawks (*Buteo swainsoni*) and Burrowing Owls (*Athene cunicularia*) occurred along 80–100% of the remote routes but only 25–38% of the facility complex routes, respectively. Additionally, Cooper's Hawks (*Accipiter cooperii*) and Merlins (*Falco columbarius*), both of which were very rare, occurred along remote routes only (Table 2).

NEOTROPICAL MIGRANTS.—The study recorded relatively few species of Neotropical migrants ($n = 9$) that winter exclusively south of the U.S. (e.g., wintering areas 1–3 in Dobkin 1994; Table 2). Most of these were detected in equal proportion along both remote and facility complex routes. The exceptions included Swainson's Hawks, which occurred along more remote routes; Orchard Orioles (*Icterus spurius*), which occupied remote routes only; and Willow Flycatchers (*Empidonax traillii*), which occurred along facility complex routes only. The latter 2 species, however, each were represented by a single individual throughout the study period, and thus were very rare.

EXOTIC AND URBANIZED SPECIES.—Finally, species associated with human introductions, human-altered landscapes, or other human activities typically occupied facility complex routes rather than remote routes. European Starlings (*Sturnus vulgaris*), Barn Swallows (*Hirundo rustica*), House Sparrows (*Passer domesticus*), House Finches (*Carpodacus mexicanus*), Rock Doves (*Columba livia*), and Ring-necked Pheasants (*Phasianus colchicus*) either were not observed along remote routes or occupied fewer remote routes than facility complex routes (Table 2). However, a single introduced species, Gray Partridge (*Perdix perdix*), was observed along 3 remote routes only.

Effects of Year

Mean number of birds per route differed significantly among years ($F_{6,66} = 16.35$, $P < 0.001$); the greatest numbers of birds were tallied during 1990 and 1989, respectively, and the fewest birds occurred during 1988 (Fig. 2a). Average number of birds per km^2 also differed significantly among years ($F_{6,66} = 5.88$, $P < 0.001$), peaking in 1989 (Fig. 2b), although for this dependent variable year interacted with type of route (see below). Average number of species per km^2 of survey area ($F_{6,66} = 2.02$, $P = 0.075$, Fig. 2c) and species richness ($F_{6,66} = 2.13$, $P = 0.062$, Fig. 2d) did not differ significantly among years. Finally, the significant interaction between type of route and year for birds per km^2 ($F_{6,66} = 3.34$, $P = 0.006$) is apparently explained by relatively larger increases in this variable along facility complex routes in the latter years of the study (Fig. 3), which generally corresponded with cooler and wetter weather (see below).

Relationship to Weather

Some variation in bird abundance and diversity appeared to be related to weather (Table 4). The first 4 yr of the study (1985–1988)

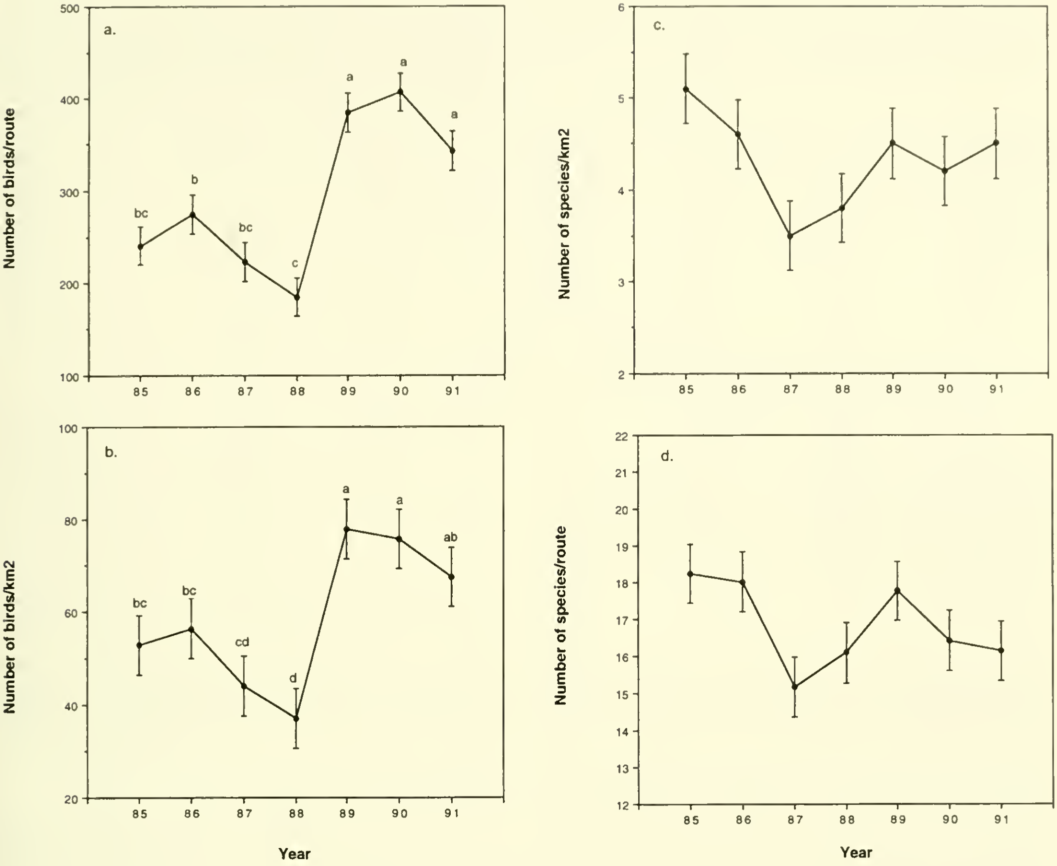

Fig. 2. (a) Number of breeding birds per route, 1985–1991, (b) number of birds per km^2 of survey area, (c) number of species observed per km^2 of survey area, and (d) number of species observed (species richness) per route. All values are $\bar{x} \pm s_{\bar{x}}$ and $n = 13$. Means that differ significantly have different letters. Note: No means comparisons were performed for number of species per km^2 or species richness because the ANOVA was not significant at the 0.05 level.

tended to be warmer and drier, while the summers of 1989–1991 were cooler and wetter. Bird abundance (mean birds/route and mean birds/km^2) was significantly correlated with average temperature, average minimum temperature, average maximum temperature, and total precipitation; that is, more birds were recorded when temperatures were lower and when precipitation was greater (Table 4). There was no relationship between bird abundance and absolute minimum and maximum temperatures for June during the study period (Table 4). Moreover, there were no relationships detected between average species richness or species per km^2 and any weather variables measured (Table 4).

Population Status and Trends for Selected Species

SAGEBRUSH OBLIGATES.—Of sagebrush-obligate species, both Brewer's Sparrows and Sage Sparrows exhibited significant positive trends in abundance (Tables 5, 6). Brewer's Sparrows exhibited positive regression coefficients across all 13 routes (5 of the individual regression analyses were significant at the 0.05 level or less), suggesting that this species increased along both remote and facility complex routes. Similarly, Sage Sparrows had positive regression coefficients for all but 1 route (a facility complex route: Radioactive Waste Management Complex), but fewer individual regressions were

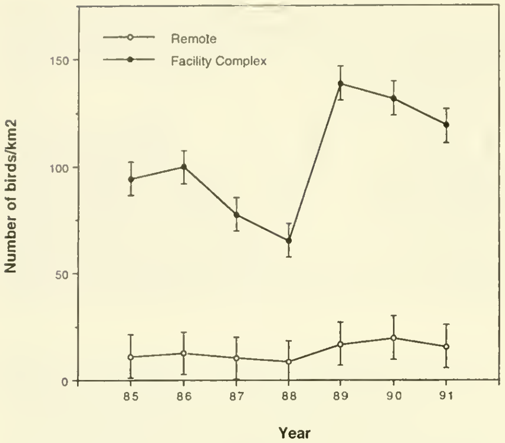

Fig. 3. Relationship between type of route (remote, facility complex) and year of survey, which interacted significantly, for the dependent variable number of birds per km^2. Means (± $s_{\bar{x}}$) for remote routes (n = 5) and facility complex routes (n = 8) are illustrated.

significant (Table 6). Sage Thrashers, while common along all routes, increased along some and decreased along others (Tables 5, 6), and there was no consistent pattern between types of route (remote routes: 3 positive, 2 negative; facility complex routes: 4 positive, 4 negative). Sage Grouse (*Centrocercus urophasianus*), also sagebrush obligates, were relatively common within the study area (Table 5); however, no trend mean could be calculated because Sage Grouse were not detected in ≥5 yr along any single route.

OTHER SHRUBSTEPPE/GRASSLAND SPECIES.—Among other common shrubsteppe species (Table 5), Western Meadowlarks, Horned Larks, Mourning Doves, and Vesper Sparrows (*Pooecetes gramineus*) had more routes with positive than negative regression coefficients and positive trend means, indicating that these species tended to increase in abundance rather than decline (Table 6). However, for none of these species was the goodness-of-fit test significant, but expected cell frequencies were low in at least some cases (e.g., for Vesper Sparrows that produced only 3 regression coefficients). Brown-headed Cowbirds and Common Nighthawks had more routes with negative regression coefficients and negative trend means, indicating that these species tended to decline in abundance over the study period (Tables 5, 6). Of the 10 routes for which cowbirds had negative coefficients, 4 were remote routes and 6 facility complex routes. Only Kyle Canyon, Idaho Chemical Processing Plant, and Radioactive Waste Management Complex routes had coefficients greater than zero. For nighthawks, 1 remote route (Twin Buttes) and 1 facility complex route (Radioactive Waste Management Complex) had positive regression coefficients, while the remainder of routes (n = 6) exhibited negative regression coefficients (Table 6).

SPECIES OF SPECIAL CONCERN.—No avian species listed as threatened or endangered by the U.S. Fish and Wildlife Service were observed, but the following species of special concern (Mosely and Groves 1994) occurred along the routes: Ferruginous Hawks (*Buteo regalis*), Burrowing Owls, Loggerhead Shrikes (*Lanius ludovicianus*), White-faced Ibis (*Plegadis chihi*), and Long-billed Curlews (*Numenius americanus*). The study recorded an average of 14 Ferruginous Hawks per year, and this species occupied all 5 remote routes and 5 of the facility complex routes (Tables 2, 5). Only 3 routes (all remote routes) provided sufficient data for analysis of trends for Ferruginous Hawks, and all 3 had regression coefficients less than zero, and 1 of these (Kyle Canyon route, P = 0.01), was significantly different from zero (Table 6). Burrowing Owls also occupied both types of routes but were much less abundant than Ferruginous Hawks (Table 5). A trend analysis could not be performed for Burrowing Owls because they were not detected along any single route for ≥5 yr. Although Loggerhead Shrikes occupied 12 of 13 routes (Tables 2, 5), only 7 routes provided sufficient data for trend analysis (Table 6). Of these routes, 3 had positive and 4 had negative coefficients, and the trend mean for Loggerhead Shrikes was negative (Table 6). Finally, White-faced Ibis (n = 1) and Long-billed Curlews (n = 3) were rare and occurred along remote routes only (Table 2), but no trend analysis could be performed for either species.

DISCUSSION

With respect to avifauna, low species richness is typical of arid and semiarid shrubsteppe and grassland habitats throughout the western United States (e.g., Wiens and Rotenberry 1981, Wiens 1985, Dobkin 1994). Moreover, these habitats support relatively few Neotropical migrants when compared to riparian or forested habitats in the same regions.

TABLE 4. Weather and climate data for the month of June and their relationship to bird abundance and richness at the INEEL, 1985–1991. All temperatures are °C, and precipitation is reported in cm. Relationships between weather variables and bird abundance and species richness are indicated by a correlation matrix showing Spearman correlation coefficients with associated *P*-values.

Year	Mean temp.	Mean min. temp.	Mean max. temp.	Max. temp.	Min. temp.	Total precip.
1985	17.0	7.6	26.4	33.9	1.7	1.0
1986	18.0	7.8	28.3	34.4	2.2	1.6
1987	17.1	7.2	27.0	33.3	–2.2	1.9
1988	19.6	8.8	30.2	37.8	0.0	0.3
1989	15.1	5.3	25.0	32.2	–3.3	3.1
1990	16.2	6.4	26.0	36.7	–1.1	2.2
1991	15.6	6.7	24.6	30.0	0.0	2.9
			Spearman Correlation Coefficients (*P*-value)			
Mean birds/route	–0.79 (0.036)	–0.82 (0.023)	–0.75 (0.052)	–0.28 (0.534)	–0.29 (0.531)	0.78 (0.036)
Mean birds/km²	–0.86 (0.014)	–0.86 (0.014)	–0.78 (0.036)	–0.43 (0.337)	–0.36 (0.427)	0.86 (0.014)
Mean species/route	–0.21 (0.644)	–0.04 (0.939)	–0.14 (0.760)	0.0 (1.0)	0.49 (0.268)	–0.04 (0.939)
Mean species/km²	–0.23 (0.613)	0.04 (0.939)	–0.23 (0.613)	–0.20 (0.670)	0.61 (0.147)	–0.02 (0.969)

TABLE 5. Mean (± *s*) number of birds per route for sagebrush-obligate species, other common shrubsteppe species, and species of special concern at the INEEL, 1985–1991. Number of survey routes along which species was recorded is indicated in parentheses. For results of trend analyses, see Table 6.

	Year						
Species	1985	1986	1987	1988	1989	1990	1991
Sagebrush obligates							
Brewer's Sparrow	9.6 ± 7.7 (13)	45.0 ± 20.1 (13)	27.2 ± 12.2 (13)	15.4 ± 14.3 (12)	74.7 ± 32.2 (13)	99.5 ± 66.9 (13)	60.3 ± 37.0 (13)
Sage Sparrow	44.6 ± 20.3 (13)	19.5 ± 12.8 (13)	18.5 ± 13.0 (13)	35.5 ± 20.1 (13)	25.5 ± 18.0 (13)	72.2 ± 39.4 (13)	71.2 ± 38.6 (13)
Sage Thrasher	26.9 ± 15.3 (13)	35.8 ± 17.6 (13)	22.5 ± 9.5 (13)	15.8 ± 6.3 (13)	22.7 ± 14.7 (13)	34.2 ± 23.0 (13)	29.8 ± 16.6 (13)
Sage Grouse	1.6 ± 1.1 (3)	5.0 ± 1.4 (2)	8.0 ± 9.0 (4)	12.8 ± 26.6 (7)	0 (0)	5.2 ± 3.4 (5)	0 (0)
Other common shrubsteppe species							
Western Meadowlark	41.1 ± 23.2 (13)	52.5 ± 20.9 (13)	30.8 ± 16.8 (13)	21.5 ± 12.0 (13)	85.6 ± 37.8 (13)	62.6 ± 35.4 (13)	51.8 ± 24.4 (13)
Horned Lark	30.1 ± 32.2 (13)	32.4 ± 43.6 (12)	45.4 ± 42.9 (13)	25.0 ± 27.0 (13)	38.6 ± 44.4 (13)	39.5 ± 48.7 (12)	52.1 ± 61.6 (13)
Mourning Dove	8.1 ± 6.0 (12)	8.6 ± 8.2 (12)	14.5 ± 15.0 (11)	7.5 ± 5.7 (10)	16.5 ± 15.7 (13)	18.6 ± 19.6 (13)	9.5 ± 7.4 (11)
Brown-headed Cowbird	19.8 ± 24.3 (11)	10.6 ± 7.7 (13)	13.9 ± 11.1 (13)	6.4 ± 7.8 (11)	9.7 ± 5.8 (13)	7.0 ± 6.7 (12)	4.8 ± 2.5 (12)
Common Nighthawk	10.4 ± 8.3 (8)	6.0 ± 5.9 (11)	5.7 ± 2.4 (9)	11.8 ± 8.2 (11)	4.8 ± 5.6 (9)	9.8 ± 11.2 (8)	4.9 ± 3.6 (9)
Vesper Sparrow	1.8 ± 1.8 (5)	2.0 ± 1.0 (3)	4.5 ± 4.9 (2)	7.0 ± 7.1 (2)	8.3 ± 7.9 (11)	4.0 ± 1.4 (4)	24.4 ± 25.4 (7)
Species of special concern							
Ferruginous Hawk	2.8 ± 3.0 (5)	3.2 ± 3.3 (5)	3.6 ± 2.6 (5)	3.5 ± 2.1 (4)	2.8 ± 1.5 (5)	2.8 ± 1.7 (4)	2.0 ± 2.0 (4)
Loggerhead Shrike	5.9 ± 3.0 (11)	5.3 ± 4.0 (9)	5.9 ± 5.4 (9)	2.6 ± 2.6 (5)	2.4 ± 1.5 (8)	5.2 ± 5.5 (9)	3.5 ± 1.9 (10)
Burrowing Owl	1.3 ± 0.5 (6)	4.0 (1)	0 (0)	0 (0)	1.0 (1)	0 (0)	0 (0)

TABLE 6. Results of trend analyses (regression coefficients) for selected species at INEEL, 1985–1991. For each species, the 1st line summarizes analyses of total birds per route, and the 2nd line summarizes analyses of birds per km². *P*-values for individual regression analyses are in parentheses. Also summarized are the number of positive and negative regression coefficients for each species and results of χ^2 goodness-of-fit tests using the Yates correction for continuity. Columns with no data represent routes where the species of interest was not detected in at least 5 survey years.

	Remote routes[a]					Facility complex routes										
Species	TB	LR	KC	CB	TF	ICPP	TRA	CFA	NRF	TAN	PBF	RWMC	ANL-W	Trend mean	No. pos./ no. neg.[b]	χ^2
SAGEBRUSH OBLIGATES																
Brewer's Sparrow	5.5	11.2	5.1	16.9	24.1	11.9	26.9	7.0	6.4	13.2	9.9	2.2	2.9	11.02	13/0	11.08***
	0.2	0.4	0.2	0.7	1.0	5.9	10.4	2.0	4.0	2.7	4.4	1.5	2.0	2.74		
	(.36)	(.26)	(.41)	(.05)	(.02)	(.05)	(.08)	(.10)	(.03)	(.12)	(.03)	(.17)	(.34)			
Sage Sparrow	8.6	14.2	7.2	10.6	8.5	2.0	12.5	7.9	0.1	9.7	7.0	−0.7	1.7	6.86	12/1	7.69**
	0.3	0.6	0.2	0.4	0.3	1.0	4.8	1.9	0.1	2.0	3.1	−0.5	0.3	1.20		
	(.15)	(.10)	(.25)	(.06)	(.22)	(.39)	(.09)	(.13)	(.97)	(.14)	(.07)	(.67)	(.33)			
Sage Thrasher	−1.8	4.5	−5.3	0.9	6.4	0.8	−0.1	1.0	−1.4	−2.1	1.9	0.0	−2.2	0.20	7/6	0.31
	−0.1	0.2	−0.2	0.0	0.2	0.4	−0.1	0.1	−0.8	−0.4	0.8	0.0	−1.5	−0.09[c]		
	(.52)	(.16)	(.11)	(.77)	(.22)	(.68)	(.94)	(.69)	(.08)	(.53)	(.19)	(.96)	(.16)			
OTHER COMMON SHRUBSTEPPE SPECIES																
Western Meadowlark	−0.9	−1.8	0.5	7.4	6.4	1.9	12.6	1.7	7.2	−2.3	8.0	3.2	6.0	3.83	10/3	2.77
	−0.1	−0.1	0.0	0.3	0.3	0.9	4.9	0.2	4.5	−0.5	3.5	2.2	4.2	1.57		
	(.90)	(.65)	(.95)	(.30)	(.46)	(.48)	(.05)	(.66)	(.16)	(.66)	(.11)	(.26)	(.14)			
Horned Lark	2.8	0.2	−2.1	5.4	11.7	2.0	5.1	3.0	1.2	7.4	−0.9	−0.3	−1.9	2.58	9/4	1.23
	0.1	0.0	−0.1	0.2	0.5	1.0	1.7	0.5	0.8	1.5	−0.4	−0.2	−1.0	0.35		
	(.63)	(.72)	(.56)	(.26)	(.03)	(.34)	(.36)	(.26)	(.58)	(.40)	(.61)	(.84)	(.59)			
Mourning Dove	2.3	2.5	2.6	3.1	1.8	—	0.4	0.4	−0.1	−0.1	0.1	0.2	−0.3	1.07	9/3	2.08
	0.1	0.1	0.1	0.1	0.1	—	0.3	0.0	−0.2	−0.1	0.0	0.1	−0.2	0.04		
	(.50)	(.12)	(.38)	(.07)	(.64)	(—)	(.35)	(.58)	(.66)	(.88)	(.91)	(.68)	(.67)			
Brown-headed Cowbird	−1.9	−2.0	0.1	−1.9	−2.4	0.5	−0.1	−4.5	−0.7	−0.3	−1.4	0.3	−8.4	−1.74	3/10	2.77
	−0.1	−0.1	0.0	−0.1	−0.1	0.3	−0.1	−2.1	−0.4	−0.1	−0.6	0.2	−5.8	−0.69		
	(.10)	(.25)	(.90)	(.38)	(.36)	(.48)	(.98)	(.31)	(.35)	(.59)	(.17)	(.69)	(.09)			

TABLE 6. Continued.

	Remote routes[a]					Facility complex routes										
Species	TB	LR	KC	CB	TF	ICPP	TRA	CFA	NRF	TAN	PBF	RWMC	ANL-W	Trend mean	No. pos./ no. neg.[b]	χ^2
OTHER COMMON SHRUBSTEPPE SPECIES																
Common Nighthawk	0.0	–2.1	–0.4	–0.6	–0.4	—	—	—	–0.9	—	—	1.1	–1.5	–0.62	2/6	1.12
	0.0	–0.1	–0.1	–0.1	–0.1	—	—	—	–0.5	—	—	0.8	–1.0	–0.12		
	(.99)	(.10)	(.08)	(.68)	(.67)	(—)	(—)	(—)	(.44)	(—)	(—)	(.30)	(.53)			
Vesper Sparrow	—	—	11.2	—	4.5	—	—	—	—	5.9	—	—	—	7.21	3/0	1.30
	—	—	0.4	—	0.2	—	—	—	—	1.2	—	—	—	0.61		
	(—)	(—)	(.01)	(—)	(.04)	(—)	(—)	(—)	(—)	(.27)	(—)	(—)	(—)			
SPECIES OF SPECIAL CONCERN																
Ferruginous Hawk	–0.3	—	–0.7	–0.3	—	—	—	—	—	—	—	—	—	–0.43	0/3	1.30
	–0.1	—	–0.1	–0.1	—	—	—	—	—	—	—	—	—	–0.02		
	(.16)	(—)	(.01)	(.49)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)			
Loggerhead Shrike	–1.0	—	1.1	0.4	—	—	—	0.2	—	–0.3	–1.2	–0.9	—	–0.23	3/4	0.00
	–0.1	—	0.1	0.1	—	—	—	0.1	—	–0.1	–0.5	–0.6	—	–0.16		
	(.36)	(—)	(.31)	(.18)	(—)	(—)	(—)	(.72)	(—)	(.37)	(.08)	(.19)	(—)			

** = $P < 0.01$; *** = $P < 0.001$. Critical value $\chi^2_{0.05}$ with 1 df = 3.841.

[a] Correspond to routes listed in Table 1.

[b] Number of routes with positive regression coefficients/number of routes with negative regression coefficients.

[c] Difference in sign results from rounding.

For example, although more than 50 species of Neotropical migrants may breed in various parts of the Intermountain West shrubsteppe, the typical community has 2–7 regular breeders, with 100–600 birds/km^2, and over half of all individuals belong to the most common species (Bock et al. 1993). Results from our study indicate that richness and density of birds at the INEEL are relatively low as well, as each route supported an average of 13–22 species and 11–169 individuals/km^2 for the 7 yr of the study. Although 90 different species were recorded, the 5 most abundant species accounted for 72% of all individuals, and over 40% of all species were represented by fewer than 10 individuals. Despite the low number of species, the INEEL does provide important habitat for several species that depend largely on sagebrush communities (e.g., Brewer's Sparrows, Sage Sparrows, Sage Thrashers, Sage Grouse), some of which have experienced declines in many portions of their range (Dobkin 1994).

Ideally, to assess the significance of trends in population numbers, one should have data from many years, over which biases related to effects of short-term variation can be minimized or eliminated. Because the current study was of relatively short duration, the trends in abundance we calculated for each species could be adversely affected by such variation. With this caveat in mind, it appears that none of the common species we examined declined significantly in abundance during the study period. In contrast, Brewer's Sparrows and Sage Sparrows apparently increased significantly in abundance during the years of the study. These increases for Brewer's and Sage Sparrows are in contrast to statewide and regional trends. Based on regional analyses of BBS data and other published information, Dobkin (1994) concluded that Sage Sparrow numbers declined in Idaho (but sample sizes were very small) and that Brewer's Sparrow numbers have declined steeply and significantly in Idaho. Declines in sagebrush-obligate species are likely related to widespread loss or fragmentation of sagebrush habitat that has occurred throughout much of the West. This habitat is being converted to grasslands via fire followed by invasion of nonnative, annual grass species (Billings 1994, Peters and Bunting 1994), or it is being converted to agriculture. Knick and Rotenberry (1995) determined that site occupancy by shrubsteppe species (e.g., Sage and Brewer's Sparrows, and Sage Thrashers) in southwestern Idaho was more probable with larger shrub habitat patches and greater total shrub cover, and by decreasing disturbance. Sagebrush-obligate species may be faring better on the INEEL because large expanses of relatively undisturbed sagebrush habitat remain.

There were significantly more species of birds and individuals per unit area along the facility complex routes. This likely reflects the different types of human activities along these routes. For example, in addition to native shrub habitat, some facility complex sites have man-made ponds while others support a variety of man-made structures, roads, and parking lots. These different land-use patterns appear to attract more species in greater density than habitats along remote routes. Remote routes traverse large expanses of mostly undisturbed habitat located in remote regions of the site. Moreover, the collection of remote routes is more homogeneous than facility complex routes (i.e., remote routes lack human structures and there is little wetland habitat along each), and this is reflected by the fact that bird abundance and species measures varied less for remote routes. In addition to increased variation in bird abundance along facility complex routes, species composition differed between remote routes and facility complex routes in several important respects. Facility complex routes supported more species of waterfowl and a larger number of "human-associated" species, while several species of raptors (Ferruginous Hawk, Burrowing Owl, Cooper's Hawk, Merlin, and Swainson's Hawk) occurred more commonly along remote routes. Such data make it clear that human activity associated with construction and operation of major facility complexes (buildings, roads, parking lots, sewage ponds, etc.) on the INEEL site affects the composition of avifauna in comparison to remote sites, although facility complex areas appear to support greater numbers of individuals.

Shrubsteppe bird populations can fluctuate independently of one another and of variation in habitat structure (Wiens et al. 1986, Bock et al. 1993), but there appears to be some association between bird abundance and plant species, their seed crops, and perhaps insect fauna (Goebel and Berry 1976, Wiens and Rotenberry 1981). However, Bock et al. (1993)

conclude that extreme and irregular fluctuation in precipitation and ecosystem productivity may be the primary factor influencing shrubsteppe avifauna. While some short-term, random fluctuations in abundance and variety of avifauna certainly are expected, results of correlation analyses suggest that some variation observed in the present study was related to weather conditions. For example, in warmer and drier years (1985–1988), fewer individuals of each species were detected, although there was no such relationship for species richness. One possible explanation for this pattern is that detectability of birds changed with weather conditions. Birds may have limited their singing or other activities during hot, dry periods, making them more difficult to census accurately using the protocol employed. However, the present study avoided at least some difficulties along these lines by performing surveys early in the day, when temperatures were more moderate. Conversely, fewer birds may have inhabited the study area or attempted reproduction during hotter, drier years. If shrubsteppe species are as highly opportunistic and ecologically adaptable as Bock et al. (1993) suggest, then more individuals would appear and attempt breeding during cooler years when precipitation is high, and when summer conditions are more favorable for reproduction (e.g., more plant cover and food, summer temperatures are less extreme). Interestingly, the significant interaction between type of route and year of study for individuals per unit area suggests that larger increases in bird density in cooler, moister years were observed along facility routes. While an explanation of this relationship is not obvious, fluctuations in avifauna were more pronounced in habitats that experienced more disturbance (i.e., along facility complex routes). Finally, because there was no relationship between species richness and weather, it appears that most of the weather-related variation among years was reflected in changes in numbers of individuals rather than in numbers of species.

Five species of special concern (Mosely and Groves 1994) were detected along the survey routes. Of these, Loggerhead Shrikes and Ferruginous Hawks were relatively common, while Burrowing Owls, White-faced Ibis, and Long-billed Curlews were rare. Previously published studies indicate that Ferruginous Hawks have declined somewhat in Idaho but increased in nearby Montana, Loggerhead Shrikes have maintained somewhat stable populations despite large annual variation, Burrowing Owls have declined steadily throughout their range, and Long-billed Curlew populations have remained stable or undergone slight declines (Dobkin 1994). Finally, White-faced Ibis populations appear to be increasing in abundance throughout many portions of their range (Sauer et al. 1997, internet access at http://www.im.nbs.gov/bbs). The 2 species for which we had adequate data, Ferruginous Hawks and Loggerhead Shrikes, had negative trend means, although the trends were not statistically significant. Nonetheless, negative trend means indicate possible declines, and more specific studies directed at these species and the land-management practices that affect them within the INEEL boundaries and elsewhere may be warranted.

In summary, the present study has provided bird population data from shrubsteppe habitats located at the Idaho National Engineering and Environmental Laboratory which will be useful for comparison with other studies in the region and future studies at the site. Analyses indicated that there are differences in avifauna between remote areas and those located near research facilities resulting from human-constructed ponds and structures and a variety of human activities. Two common shrubsteppe species (Brewer's Sparrows and Sage Sparrows) appear to have increased in abundance at the INEEL during the study period despite statewide and regional declines purportedly from destruction of sagebrush habitat. In addition to providing important large patches of habitat for a number of sagebrush-obligate species, the INEEL supported at least 5 avian species of special concern, 2 of which had negative trend means and declined in abundance along some routes.

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MITE PARASITISM OF MOSQUITOES IN CENTRAL WYOMING

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ABSTRACT.—Parasitic larval mites including *Thyasides sphagnorum* were collected from mosquitoes captured in New Jersey light traps over a period of 6 yr and from landings during 1 collecting season in Natrona County, Wyoming. Overall mite prevalence on mosquitoes was 0.42% and abundance was 0.76%. Prevalence on *Aedes dorsalis* was significantly greater than on other host species. Comparison of light trap data and landing data suggests that parasitized mosquitoes may seek blood meals more frequently than non-parasitized mosquitoes.

Key words: Hydrachnidia, Thyasides sphagnorum, Aedes dorsalis, *water mites, prevalence, mosquito parasitism.*

As scientific information has revealed environmental and health consequences of chemical control of mosquitoes, natural control of mosquitoes has become an ongoing area of study. Mosquitofish, *Gambusia affinis*, and bacterial agents, such as *Bacillus thuringiensis* var. *israelensis* and *Bacillus sphaericus*, have been developed and are widely applied to control mosquito larvae.

Larval water mites of the group Hydrachnidia (order Acariformes) are parasitic on aquatic insects, including mosquitoes (Smith 1988). In a review of all known records of mosquitoes parasitized by mites, both *Aedes dorsalis* and *Culiseta inornata* are listed as hosts for mites whose identities have not been determined. *Culex tarsalis* has been parasitized by *Piona* sp. (Mullen 1975). Tsai et al. (1969) collected ectoparasitic red larval mites (*Arrenurus* spp.) from *Ae. increpitus*, *Ae. pullatus*, and *Cs. impatiens* in southwestern Wyoming.

Smith and McIver (1984) noted that host-seeking *Coquillettidia perturbans* consistently had a lower abundance and prevalence of parasitic mites than newly emerged mosquitoes. It also appeared that the abundance of larval mites did not closely match the abundance of available hosts.

This study was conducted to investigate the prevalence and abundance of larval water mites on different species of female mosquitoes collected in Natrona County, Wyoming, to determine the potential for utilizing mites for mosquito control. Mite prevalence, abundance, and mean intensity (Margolis et al. 1982) were investigated for *Cx. tarsalis*, *Cs. inornata*, and the genus *Aedes*. Seasonal and yearly patterns were compared. Additional comparisons were made between data collected from light traps and data collected from mosquito landings on human subjects.

METHODS

Mosquitoes were trapped every night from the 1st week of June through the middle of September 1991–1996 in 5 New Jersey light traps at 4 locations in Natrona County: Casper (106°16′53″W, 42°50′05″N), Evansville (106° 15′58″W, 42°51′52″N), Vista West II (106° 26′30″W, 42°51′52″N), and Natrona County Airport (106°27′54″W, 42°53′35″N and 106° 27′24″W, 42°54′0″N) where 2 traps were located. The Evansville and Casper traps were located in residential areas. The Vista West II trap, which was in a rural irrigated subdivision, was not included in the 1991 study. One airport trap was placed next to an irrigation pond and irrigated pasture, the other next to a service building with no irrigation activity on the grounds surrounding the building. Mosquitoes were collected from the traps every Monday, Wednesday, and Friday and were sorted by sex. No male mosquitoes were included in the study. Female *Cx. tarsalis* and *Cs. inornata* were identified to species and counted. Due to time constraints and difficulty identifying some specimens to species, female members of the mosquito genus *Aedes* were grouped for counting purposes. Female

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TABLE 1. Combined results from 5 traps recorded from the 1st week of June through mid-September 1991–1996.

Mosquito species/group	Number of ♀ mosquitoes	Number of ♀ hosts	Number of mites	Mite prevalence	Mite abundance
Aedes	36,514	240	434	0.66%	1.19%
Culex tarsalis	16,861	7	8	0.04%	0.05%
Culiseta inornata	8,356	10	30	0.12%	0.36%
Total	61,731	257	472	0.42%	0.76%

mosquitoes with mites were separated and the parasite load noted. All female host mosquitoes were identified to species, including *Aedes*. Other species of mosquitoes in Natrona County are not numerous enough to be included in the study. Collections ceased the 2nd full week of September when the weather became too cold for mosquito activity.

Additionally, in 1996 mosquitoes were collected in a New Jersey light trap and during landings at another location in the county (106°16′47″N, 42°52′51″W). Landings were conducted the day following a trap night during which it was likely that parasitized mosquitoes would be captured. A Hausherr mosquito vacuum collector was used by a human subject to gather mosquitoes landing on his skin and clothing.

Statistical software in Epi Info Version 5 was used to analyze mite prevalence on mosquitoes landing on individuals versus those collected in the New Jersey light trap. This study was conducted in conjunction with the routine mosquito surveillance program of the City of Casper–Natrona County Health Department.

RESULTS

Table 1 summarizes results for 1991–1996. *Aedes dorsalis*, *Cx. tarsalis*, and *Cs. inornata* are the 3 most abundant species of mosquitoes in Natrona County. Within the *Aedes* genus *Ae. dorsalis* is most abundant, comprising approximately 90–95% of this group in Natrona County (unpublished data). For *Aedes* the only species found to be parasitized was *Ae. dorsalis*. Mean parasitic intensities for the 3 groups were *Aedes*, 1.81; *Cx. tarsalis*, 1.14; and *Cs. inornata*, 3.00. Mite intensity varied from 1 to as many as 9 mites per host. *Cs. inornata* had the greatest mean intensity and is the largest mosquito in size. No other species of mosquitoes were parasitized by mites. Larval mites were observed attached to male mosquitoes when sorting collections, but these were not included in the study.

Two larval mites collected from *Ae. dorsalis* were identified as *Thyasides sphagnorum* by Bruce P. Smith. Mites were most commonly found attached to the posteroventral region of the thorax near the junction of the abdomen (89%), followed by attachment at the neck region.

For each year of the study both mite prevalence and mite abundance were greatest on *Aedes* spp. Although all *Aedes* species were grouped for counting purposes, only *Ae. dorsalis* were found to be parasitized by mites; therefore, actual prevalence and abundance figures for *Ae. dorsalis* are somewhat greater than indicated in Table 1. Statistical analysis of host selection demonstrated significantly higher parasitism by mites on *Ae. dorsalis* ($\chi^2 = 76.69$, $P < 0.0001$).

Over the 6 yr of the study, mites were collected from mosquitoes as early as 20 May and as late as 18 September. However, parasitism by mites tended to occur over a 2-mo period each summer, with the time of onset varying from late May to July. Overall, 50% of the mites were recovered during June; however, in 1993, when the smallest number (17) of mites was collected, 70% (12) of those were found on mosquitoes in August. Mite specimens collected early each year tended to be engorged, whereas those collected later in the season tended to be smaller and not engorged.

Prevalence of mites collected from mosquitoes captured while landing on human subjects was significantly greater than from mosquitoes in New Jersey light traps at the same location (Table 2). Prevalence was 2.5% from the light trap and 14.6% from landings. The Fisher exact P value = 0.0001728.

TABLE 2. Mite prevalence on female *Ae. dorsalis* captured in New Jersey light traps versus mite prevalence on female *Ae. dorsalis* captured during landings. Landings were conducted the day following the trap night.

	New Jersey trap			Landings		
Trial	*Ae. dorsalis*	Hosts	Mites	*Ae. dorsalis*	Hosts	Mites
1	215	2	2	36	4	7
2	10	0	0	30	6	16
3	7	1	1	3	1	3
4	9	3	8	13	1	1
Total	241	6	11	82	12	27

DISCUSSION

Results of this study indicate that larval water mites, including *T. sphagnorum*, may prefer *Ae. dorsalis* as a host and that the mite population may be dependent upon a large host population of *Ae. dorsalis*. Because *Ae. dorsalis* is the most abundant mosquito species in Natrona County and this species is multivoltine, the likelihood of mites attaching to emerging members of this species is high. Females of this species would also be expected to return to aquatic oviposition sites in a single season, whereas both *Cx. tarsalis* and *Cs. inornata* overwinter as females (Harmston and Lawson 1967), returning the subsequent season to aquatic sites for oviposition. Consequently, larval mites selecting *Ae. dorsalis* as a host would have greater success returning to an aquatic environment. All 3 mosquito species have been collected from the same aquatic habitat, although seasonal differences in species abundance occur (unpublished data).

Mite prevalence on *Aedes* in 1993 was the lowest of the 6-yr study. However, in 1993 *Aedes* spp. were only 41% of the total counted mosquito population compared to an average of approximately 60% for all years combined. Additionally, most mites were collected from hosts in August and September 1993 when *Cs. inornata* and *Cx. tarsalis* comprised greater percentages of the mosquito population. A reduced population of the preferred host and a later appearance of larval mites may have reduced successful attachment.

Mosquito numbers were highest in 1994, likely due to the large number of *Aedes* (78% of all mosquitoes trapped). The greatest number of mites was also collected that year. Interestingly, during 1994 no water mites were collected from either *Cx. tarsalis* or *Cs. inornata*, perhaps due to the greater abundance of *Ae. dorsalis* available to serve as hosts. In 1994 precipitation was low (National Weather Service data), which led to increased irrigation activity (Alcova Irrigation District personal communication). *Aedes dorsalis* is often associated with irrigated crops and pastures (Denke and Spackman 1990).

Mite prevalence and abundance figures reported in this study may be low if mite specimens were dislodged from hosts while in the collecting jars. It is suspected this occurred, especially on nights when mosquito collection numbers were high.

Mullen (1977) also reported the prevalence of parasitism by *Thyasides sphagnorum* in the northeastern United States to be very low (<1.0%) on the 4 species of *Aedes* and 1 species of *Culiseta* parasitized by *T. sphagnorum* in New York.

Mosquitoes that were collected as they landed on humans, presumably to feed, had a higher prevalence of mites than those collected from light traps at the same location. There are 2 possible explanations for this. One is that the flight of parasitized mosquitoes is hindered by attached mites, and consequently these mosquitoes are more easily captured. Alternatively, parasitized mosquitoes are feeding more frequently to compensate for nutritional loss due to mites. *Anopheles crucians*, when parasitized by the water mite *Arrenurus pseudotenuicolis*, was found to feed more frequently than non-parasitized mosquitoes (Lanciani and Boyt 1977).

If the initial hypothesis is correct, parasitized mosquitoes may suffer increased mortality due either to a slower response by the mosquito to its host defense mechanism or to predation. If the latter is true, the nuisance capability of an individual parasitized mosquito may be greater than that of a non-parasitized mosquito.

Last, if parasitized female mosquitoes need more blood meals to compensate for nutritional loss to mites, they may be visiting more hosts, making them more effective disease vectors. *Aedes dorsalis* is considered a vector of California encephalitis (Crane et al. 1977, Moore et al. 1993). It may be that parasitized mosquitoes bite more frequently but also have a lower survivorship than non-parasitized mosquitoes.

Low mite prevalence and abundance demonstrated in this study indicate no potential for successfully utilizing mites as a control agent.

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VEGETAL CHANGE ON A NORTHERN UTAH FOOTHILL RANGE IN THE ABSENCE OF LIVESTOCK GRAZING BETWEEN 1948 AND 1982

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ABSTRACT.—Reexamination of a semiarid foothill rangeland, first evaluated in 1948, indicated that secondary succession continues to shift toward a perennial grass-forb community formerly dominated by xeric shrubs, particularly big sagebrush (*Artemisia tridentata* spp. *vaseyana*). The direct role of livestock grazing in establishment and maintenance of shrub-dominant plant communities appears confirmed in the decline of shrubs upon cessation of livestock grazing in summer and continued browsing by mule deer in winter. The reduction of shrub forages on mule deer winter ranges is a major factor in population declines.

Key words: vegetation change, livestock grazing, succession, mule deer.

Evaluation of presettlement vegetation on foothill ranges in the northeastern Great Basin indicates relative dominance of herbaceous grasses and forbs over shrubs (Simpson 1876, Leopold 1950, 1959, Passey and Hugie 1962, Christensen and Johnson 1964, Hull and Hull 1974, Vale 1974). Generally, perennial grasses and forbs dominated plant communities on more mesic foothills, whereas shrubs such as Vasey's big sagebrush (*Artemisia tridentata vaseyana* [Rybd.] J. Boivin), saltbush (*Atriplex* spp. L.), and greasewood (*Sarcobatus vermiculatus* [Hook] Torr.) were more abundant on xeric and/or saline valley-floor sites at mid-19th century (Stewart 1941, Vale 1975, Urness 1976).

Rapid proliferation of livestock—cattle, horses, and sheep—after about 1860 altered this dynamic equilibrium by reducing palatable herbaceous forages and decreasing fire frequency, allowing increases in less palatable and fire-susceptible shrubs. Changes in plant communities were rapid. Shrub dominance became common on Utah foothills by the early 20th century on lands not preempted for agriculture (Julander 1962). Concurrent with the increase of shrubs on winter ranges, after hunting regulations ended excessive exploitation about 1910, mule deer (*Odocoileus hemionus* Rafinesque) populations gradually expanded (Leopold 1959, Hancock 1981).

Unless site potentials are unalterably degraded, retrogression of plant community composition can be halted and reversed; that is, elimination of the processes that initiated change can facilitate secondary succession proceeding back toward a condition similar to what previously existed (Ellison 1954, 1960, Robertson 1971, Rogers 1982). However, plant communities will not necessarily duplicate presettlement vegetation in Great Basin sagebrush-grass types due to introduction of adapted annual and biennial weeds such as cheatgrass (*Bromus tectorum* L.), Dyer's woad (*Isatis tinctoria* L.), and a myriad of others (Young et al. 1976, Blaisdell et al. 1982, Young and Sparks 1985:234, Burger et al. 1986).

An example of remarkably rapid secondary succession on a northern Utah foothill range was reported by Smith (1949). Land between Green and Logan canyons, Cache County, was purchased by the Utah Game and Fish Department (now Division of Wildlife Resources, DWR) in 1937 as critical deer winter range. Summer use by cattle was immediately terminated on the DWR property but not on adjacent private land. Smith measured vegetational differences that had occurred between 1937 and 1948 on the 2 parcels. This paper reports on a reexamination of the same areas in terms of available vegetation in 1982 after an additional 34 yr of deer-only use on the DWR property (deer range) and after livestock use had ceased for about 25 yr on the private (livestock range) area.

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STUDY AREA

The foothills between Green and Logan canyons lie on the uppermost bench terrace of Pleistocene Lake Bonneville at about 1525 m elevation (T12N R1E Salt Lake Meridian, SW 1/4 sec. 24 and NW 1/4 sec. 25). Deer concentrate on this area as traditional winter range and, since curtailment of livestock grazing, constitute the major impact on vegetation. Smith (1949) reported the composition of plant communities under heavy summer livestock grazing was dominated by big sagebrush, but contained elements of perennial grasses and forbs putatively prominent in the presettlement condition (Hull and Hull 1974). Important grasses included Sandberg's bluegrass (*Poa secunda*) and bluebunch wheatgrass (*Elymus spicatus*); perennial forbs were arrowleaf balsamroot (*Balsamorhiza sagittata*), mulesears (*Wyethia amplexicaulis*), and one-head sunflower (*Helianthella uniflora*).

According to Erickson and Mortensen (1974), soils are limestone-derived Lithic Xerorthents on steeper slopes over 20% (Richmond series, upland very gravelly loams) and Typic Calcixerolls on slopes of 10–20% (Sterling series, gravelly loams). Aspect is west-facing. Summers are hot and dry; winters, cold and moist. Precipitation averages 468 mm annually (29-yr record), over 2/3 of which occurs between October and April. The excessively well-drained character of these gravelly or cobbly soils combined with high evaporation reduces effectiveness of precipitation during the growing season, thus resulting in dry range sites of limited productivity.

METHODS

Because plots were not permanently marked in the original study (Smith 1949), exact relocations were impossible. However, rematch of photos allowed us to closely approximate transect sites (personal communication and onsite tour with A.D. Smith, Rangeland Resources Department, Utah State University, June 1982). The same sampling procedures for density were followed in 1948 and 1982 to assure comparable data sets:

> In June, 1948, vegetation data were secured from a series of 100 square foot plots on each side of the fence, which as far as livestock are concerned, separates the area into two zones. One series of plots was distributed along a transect roughly at right angles to the division fence. Another pair of transects was extended parallel to the fence crossing the first transect at right angles. One of these was within the deer range and the other in the cattle range. Seventy plots were delimited in each area. Vegetation data were recorded as number of individuals of each species (Smith 1949).

Because the original 1948 data were not available, statistical comparisons between years were not possible. Data between treatments in 1982 were analyzed by standard *t* test of the means.

RESULTS AND DISCUSSION

Density changes among years, major plant species, and treatments are summarized in Table 1. This is not a complete listing, but rather a focus on important species reported in the 1948 analysis (Smith 1949). The main observations in 1948 on the livestock-excluded deer range were the increase of some perennial grasses and forbs and the simultaneous decline of shrubs, especially big sagebrush, after only 11 yr. The 1982 data demonstrated that earlier trends had continued on the deer range for arrowleaf balsamroot, bluebunch wheatgrass, and Sandberg's bluegrass. Of critical importance, big sagebrush was absent. Indeed, no evidence of dead big sagebrush plants remained on the deer range, and, without the earlier documentation, one could easily conclude big sagebrush had never been available. Moreover, in 1982 the livestock range, grazed by cattle from 1948 to 1957, appeared similar to the deer range in 1948, especially with respect to dead and live big sagebrush. It is predictable that with additional years of non-use by livestock in summer, the livestock range will progress toward vegetation composition and structure now present in the deer range.

These vegetational changes occurred in certain absence of fire, herbicidal application, reseeding, or other range management treatments. Thus, it appears that livestock grazing of grasses and forbs during the summer growing season shifted the competition advantage to shrubs and was the primary factor driving succession toward woody plant dominance. Numerous studies support our findings that spring-summer livestock grazing maintains or improves shrub stands on big game winter ranges (Mueggler 1950, Smith and Doell 1968, Jensen et al. 1972, Harniss and Wright 1982,

TABLE 1. Number of plants found in a series of seventy 100-ft^2 plots on adjacent ranges grazed by deer in winter (deer range) and by livestock in summer and deer in winter (livestock range). The livestock range ceased to be grazed by livestock in 1957, and both were remeasured in 1982.

	1948				1982			
	Deer range		Livestock range		Deer range		Livestock range	
	Total plants	Number of plots upon which plants occurred	Total plants	Number of plots upon which plants occurred	Total plants	Number of plots upon which plants occurred	Total plants	Number of plots upon which plants occurred
FORBS								
Achillea millefollium L.[a]	—	15	—	36	—	11	—	29
Agoseris glauca (Pursh) Raf.	88	16	0	0	0	0	11	6
Balsamorhiza sagittata (Pursh) Nutt.	676	47	96	17	1696	70	704	53
Helianthella uniflora (Nutt.) T.&G.	243	31	3	3	140	26	75	11
Heliantus annus L.	0	0	69	3	0	0	0	0
Wyethia amplexicaulis (Nutt.) Nutt.	64	1	8	5	5	2	6	4
GRASSES								
Elymus spicatus (Pursh) Gould	24	14	9	8	136	28	398	62
Koeleria macrantha (Ledeb.) Schultes	8	3	1	1	3	3	12	6
Poa pratensis L.[a]	—	3	—	2	—	2	—	11
Poa secunda Presl.[a]	1610	68	667	64	2040	68	1750	69
BROWSE								
Artemisia tridentata (dead) Nutt.	185	64	92	38	0[b]	0	122	56
Artemisia tridentata (live) Nutt.	88	38	580	64	0[b]	0	98	39
Chrysothamnus nauseosus (Pallas) Britt.	2	2	8	16	0	0	0	0
Gutierrezia sarothrae (Pursh) Britt. & Rusby	29	8	185	33	1[b]	1	128	27

[a] Occurred as small patches only.

[b] Numbers of plants between deer and livestock range in 1982 were significantly different ($P < 0.05$).

Reiner and Urness 1982, Stevens 1986, Austin and Urness 1995). Conversely, removal of livestock grazing causes increasing grasses and forbs and decreasing shrubs (Laycock 1967, Anderson and Holte 1981, Austin et al. 1986). The net effect on foothill rangeland without livestock grazing is that single use by mule deer in winter will gradually impose successional changes that adversely affect deer habitat carrying capacity. Deer range values on this study site have greatly decreased from 1937 to 1948 to 1982.

Similar trends observed over many mule deer ranges in western United States, where summer grazing by livestock has been eliminated or greatly curtailed, give reason for concern about the future of many deer herds (Julander and Low 1976, Anderson and Holte 1981, Hancock 1981, Austin et al. 1986, Clements and Young 1997). Certainly, mule deer herds reached peak numbers in the early 1950s and have since declined throughout the Intermountain West (Julander and Low 1976, Hancock 1981). Managed livestock grazing on foothill ranges (Anderson and Scherzinger 1975, Austin et al. 1983) is a logical managerial solution to the decline of winter range habitat and mule deer numbers.

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ARDEN R. GAUFIN, 1911–1997: OBITUARY AND LIST OF PUBLICATIONS

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Arden R. Gaufin

Arden R. Gaufin was born in Salt Lake City, Utah, on 25 December 1911, and passed away on 8 January 1997. He married Ruth Lund in September 1936 and to them were born two children: Richard and Marilyn. Raised on a farm in Kaysville, Utah, Arden graduated from Davis High School. He attended the University of Utah, receiving both his B.S. and M.S. degrees in biology, and then went to Iowa State University, where he received his Ph.D. in 1950. His doctoral dissertation was a study of the production of the bottom fauna of the Provo River, Utah. He served as a captain in the U.S. Army in the South Pacific during World War II and received the Bronze Star.

Arden's first position after graduating was with the Public Health Service Environmental Health Center in Cincinnati, Ohio. There he met Clarence Tarzwell and together they championed the idea that aquatic insects are actually twenty-four-hour instream sentinels of stream conditions. Their research on Lytle Creek, Ohio, was very significant in the formulation of the design, methodology, and implementation of research on and recognition of the importance of sampling aquatic environments. Such studies stressed the importance of complementing physical and chemical data with biological information. Results of this applied research helped strengthen the need to protect aquatic life, the true indicators of environmental health. This in turn led to the establishment of water quality criteria for protecting the integrity of aquatic ecosystems at the time when states were formulating stream standards for inter- and intrastate waters.

As a result of his research on integrating the physical, chemical, and biological components of aquatic systems, Arden was selected to serve on the Public Health Service National Advisory Council, which established water pollution control standards in the 1960s. It was during this time that Arden became one of the early members of the Midwest Benthological Society. He was an avid supporter of and participator in this organization that is now the very successful North American Benthological Society.

Arden was a Professor of Biology from 1953 to 1975 at the University of Utah, where he taught a wide variety of classes. He spent the summers from 1963 through 1975 at the University of Montana Biological Station on Flathead Lake as Visiting Professor of Zoology and Assistant Director. In addition, he worked during the 1968–69 school year at the University of Montana campus in Missoula as Professor of Zoology and Director of Environmental

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Biology. The summers in Montana and the nearby states and Canadian provinces were some of the highlights of Arden's life. The biological station experiences reminded him of the summer that he spent as a graduate student at the University of Michigan, Douglas Lake Biological Station.

Over the years Arden guided many graduate students in a wide variety of projects dealing with aquatic ecosystems. His interests ranged from high mountain lakes to salt ponds near the Great Salt Lake. In fact, many colleagues would say that Arden's greatest contribution to aquatic biology is the large number of students he influenced. He was always ready to listen to novel ideas and would willingly seek funding to support a new graduate student. His help extended not only to those included as coauthors in the following list of publications but also to numerous others who studied various aspects of aquatic biology. Arden helped many students begin successful careers in biology. For this we owe him a lasting debt of gratitude.

In addition, he worked with several colleagues on projects across the United States: C.M. Tarzwell, stream pollution in Ohio; R. Patrick, macroinvertebrates and algae of the Potomac River; G.W. Prescott, algae in and around Flathead Lake, Montana; J.F. Hanson, S.G. Jewett, Jr., and W.E. Ricker, stoneflies (Plecoptera).

Several of Arden's former graduate students aided in the preparation of this publication. Their help and encouragement are much appreciated: Claron Bjork, Price, Utah; Allen Knight, Green Valley, Arizona; Alan Nebeker, Corvallis, Oregon; Jack Stanford, Polson, Montana; Gerald Smith, Ann Arbor, Michigan; Bill Stark, Clinton, Mississippi.

Following is a list of scientific publications authored by Arden or coauthored by him with colleagues and students. Even though every attempt was made to maintain consistency, some problems still exist because original publications were not available.

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BOOK REVIEW

Wild Plants and Native Peoples of the Four Corners. William W. Dunmire and Gail D. Tierney. Museum of New Mexico Press, Santa Fe, NM 87504. 1997. $22.50, softcover.

This is a handsomely produced, well-edited volume that provides authoritative commentary on both native peoples and the indigenous plants used by those peoples in the Four Corners area of the American Southwest. The informative and interesting narrative is supported and enriched by 117 photographs (90 in color and 27 in black and white). The quality of photo reproduction is outstanding. Separate chapters introduce the reader to 4 native peoples still inhabiting the area: the Hopi, Navajo, Ute Mountain Ute, and Jicarilla Apache. Although brief, these chapters provide the reader with carefully selected, reliable information concerning the history, geographic distribution, culture, and ethnobotany of each ethnic group. Photographs support the written discussions of each native culture.

Fifty of the plants most frequently used by native peoples are treated individually and in considerable detail. Each species, illustrated by well-executed line drawings and/or color photos, is discussed in terms of cultural uses and occurrence at 5 national parks (Aztec Ruins, Canyon de Chelly, Chaco Canyon, Hovenweep, and Mesa Verde) where one can see the physical remnants of and acquire detailed information concerning the peoples discussed in this book. Specific uses of each species are enumerated, and techniques employed in their collection and preparation are often given. In addition, the authors provide useful references for researchers desiring to pursue a topic in greater depth. An appended "Annotated List of Useful Plants" treats over 500 species, listing their uses in each of 7 categories (basketry, ceremonial uses and tools, cordages or matting, dyes and paints, foods and materials for smoking, medicine, and structural timber or fuel) and 5 cultures (Hopi, Jicarilla Apache, Navajo, southern Paiute, and Ute). Each use/culture listing is documented by 1 of 40 original references included in cited literature.

Any massive effort such as that attempted in this pocket-size handbook (300 pages of 5 1/2 × 8 1/2 inches) will, of necessity, leave some questions unanswered and include some statements with which other specialists will quibble. I found myself wishing to see clinical evaluations of the numerous curative and salutary effects reported for the 423 species listed as having been used medicinally. Certainly not all those species were effective treatments for the numerous and disparate maladies they were used against. Likewise, some statements concerning individual plants should be accepted with caution. I question the author's assertion that *Phoradendron* mistletoe "does not really harm" host juniper trees. By the same token, I question whether pseudoephedrine is produced by any native American species of *Ephedra*. Of perhaps more importance, I thought the authors dismissed too easily the potential toxicity of crushed chokecherry pits. Pulverized chokecherries (cherries and pits) have caused deaths among Ute Indians of northeastern Utah when added to fresh pemmican.

My few quibbles notwithstanding, I highly recommend this book for the libraries of all interested in native peoples of the Four Corners area. For professional archaeologists and ethnobotanists, the book will be essential reading. I do not know of another single source that is so packed with valuable, reliable information concerning the ways in which native peoples have used the native flora to facilitate their survival.

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INFORMATION FOR AUTHORS

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GAP ANALYSIS OF THE VEGETATION OF THE INTERMOUNTAIN SEMI-DESERT ECOREGION

David M. Stoms[1], Frank W. Davis[1], Kenneth L. Driese[2],
Kelly M. Cassidy[3], and Michael P. Murray[4]

ABSTRACT.—A conservation gap analysis was conducted for the Intermountain Semi-Desert ecoregion to assess the representation of land-cover types within areas managed primarily for biodiversity objectives. Mapped distributions of plant communities were summarized by land-management status categories. The total amount of land permanently protected in the ecoregion is <4%, and most types that are characteristic of the region have <10%. Of 48 land-cover types, 20 were found to be particularly vulnerable to potential loss or degradation because of low level of representation in biodiversity management areas and the impact of expected land-use activities. Gap analysis data and findings will be useful in providing a regional perspective in project impact assessment and future conservation planning within this ecoregion.

Key words: gap analysis, land cover, land management, conservation assessment, National Vegetation Classification System, alliance.

In recognition of the alarming but largely unmeasured conversion and degradation of native habitat, many conservation biologists have recommended protecting representative samples of all natural ecological communities as a goal for preserving biological diversity (e.g., Shelford 1926, Committee on the Study of Plant and Animal Communities 1950–51, Austin and Margules 1986, Shafer 1990, Scott et al. 1993). Underlying this "coarse-filter" approach is the assumption that protecting ecosystems or habitats will simultaneously confer protection on most plant and animal species (Noss 1987, Franklin 1993, Orians 1993). While this approach sounds straightforward in principle, a lack of comprehensive and consistent data on the extent, location, and management of ecological communities makes it quite challenging to implement. Fundamental questions have often been beyond our capacity to answer with any confidence; for example, How well are community types represented in areas specially managed for the preservation of biodiversity?

Scott et al. (1993) outlined a "gap analysis" methodology to identify the underrepresented

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plant communities, or gaps, in the representation of biological diversity in areas managed primarily for long-term maintenance of native wildlife populations and natural ecosystems. This approach uses medium-scale mapping of land cover and land management as the only practical solution for assessing the conservation status of biodiversity across ecological regions covering hundreds of thousands of square kilometers. Originating as a pilot study in Idaho (Scott et al. 1993, Caicco et al. 1995), gap analysis has been expanded into a national Gap Analysis Program (GAP) coordinated by the Biological Resources Division of the U.S. Geological Survey (formerly the National Biological Service). Initial published results have focused on analyses at the state level for Idaho (Caicco et al. 1995), Utah (Edwards et al. 1995), and Wyoming (Merrill et al. 1996). Since its inception, however, GAP has aimed to provide a national conservation assessment based on ecological rather than political planning regions (Scott et al. 1993).

The objective of this paper is to report the results of the nation's first multistate gap analysis of plant communities of the Intermountain Semi-Desert (ISD) ecoregion (Fig. 1) as currently delineated in the U.S. Forest Service's ECOMAP program (ECOMAP 1993, Bailey 1995). Ownership and management status of land-cover types within the ISD ecoregion (and 2 subregions) are summarized, poorly represented types are identified, and the highest conservation priorities are identified. Secondarily, we discuss some ecological and cartographic issues of this approach to regional conservation assessment. Technical aspects of regional mapping will be treated in Stoms et al. (in press). Although gap analysis as defined by Scott et al. (1993) typically includes vertebrate species distributions, here we report only plant community types.

This ecoregion was selected for the prototype regional gap analysis for both practical and conservation reasons. From a practical standpoint, the ISD ecoregion was among the first for which the requisite land-cover and land-management mapping were completed by individual state-level GAP projects. Additionally, the area provides a suitable testing ground for demonstrating whether GAP can overcome technical challenges associated with regional mapping that have concerned some program reviewers (Zube 1994, DellaSala et al. 1996). Very little land in the ISD ecoregion has been designated for maintenance of biodiversity, while potentially conflicting land uses such as grazing and cultivation are extensive. Enough undeveloped habitat remains, however, for proactive conservation action to be effective. Thus, the ISD ecoregion makes a representative case study that could be applied to other regions throughout the western U.S. Planning for conservation and ecosystem management within this ecoregion is underway by The Nature Conservancy (Sandy Andelman personal communication), Oregon Biodiversity Project (Vickerman 1996), and Interior Columbia Basin Ecosystem Management Project (a joint effort by the U.S. Forest Service and Bureau of Land Management; Quigley et al. 1996). BLM is considering wilderness proposals in Wyoming (Merrill et al. 1996). Proposals for new wilderness areas in Idaho (Merrill et al. 1995) and Wyoming (Merrill et al. 1996) and for new national parks (Wright et al. 1994, Wright and Scott 1996) are being discussed. A regional gap analysis can add valuable information for all of these planning programs.

INTERMOUNTAIN SEMI-DESERT ECOREGION

The U.S. Forest Service's National Hierarchical Framework of Ecological Units (ECOMAP 1993) was adopted for this ecoregional gap analysis. This division of regional units is widely used both by federal agencies and The Nature Conservancy (The Nature Conservancy Ecoregional Working Group 1996) as the basis for resource assessments. The framework subdivides the Earth's surface into successively smaller, more homogeneous land units. The highest level, called the *domain*, is associated with broad climatic regimes and gross physiography. Domains are split into *divisions* based on vegetational affinities. *Provinces* are subdivisions of a division corresponding to continental weather patterns, soil orders, and potential natural vegetation. Domains, divisions, and provinces are all categorized at the ecoregional level in the framework. Provinces can be progressively subdivided into *subregions*, *landscapes*, and ultimately *land units* at the project planning level. The ISD ecoregion used in this gap analysis is a province in the ECOMAP hierarchy.

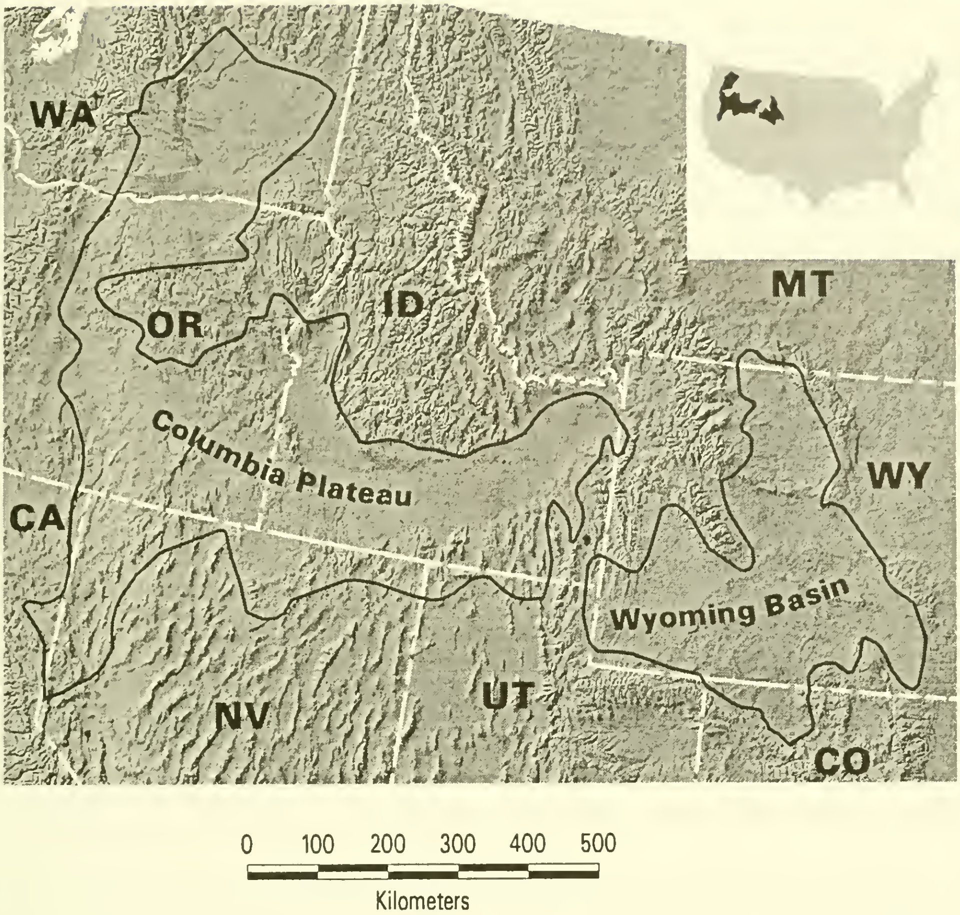

Fig. 1. Shaded relief image of the Intermountain Semi-Desert ecoregion and the 2 subregions, Columbia Plateau and Wyoming Basin.

The ISD ecoregion encompasses approximately 412,000 km^2 in portions of Washington, Oregon, Idaho, Nevada, California, Utah, Wyoming, Colorado, and Montana (Fig. 1). Two geographically disjunct subregions make up the larger ecoregion, the Columbia Plateau in the west and the Wyoming Basin in the east. The ISD boundary corresponds closely to the limits of Küchler's (1970) sagebrush steppe potential natural vegetation type. The ISD ecoregion southern boundary grades into the Intermountain Semi-Desert and Desert Province, which tends to be warmer, drier, and with greater topographic relief than the ISD ecoregion. The Cascade and Sierra Nevada ranges bound the ecoregion on the west and the northern Rocky Mountains on the north and east.

The combination of soils and climate generates a characteristic vegetation often called "sagebrush steppe" (Küchler 1970), dominated by *Artemisia* spp. or *Atriplex confertifolia* (shadscale) with short bunchgrasses (e.g., *Festuca* spp., *Pseudoroegneria* spp.). The rainshadow effect produced by the Cascade–Sierra Nevada ranges favors shrub cover and limits tree cover to higher elevations (mostly conifers and aspen), narrow riparian corridors, or sparse pinyon or juniper woodland. In low-lying alkaline areas formed in Pleistocene lake beds and subject to periodic flooding, sagebrush is replaced by saltbush (*Atriplex*) and greasewood (*Sarcobatus*) communities. Shrub species are replaced by perennial grasses where deeper soils occur. Most relatively level land with adequate water supplies has been converted to agriculture

(West 1988). Nonnative annual grasses, especially cheatgrass (*Bromus tectorum*), have invaded the region since the 1870s, successfully converting native steppe communities to exotic grassland (West 1988) and dramatically affecting ecological processes of this vegetation type. Despite the relatively homogeneous appearance of sagebrush steppe, the ecoregion is floristically complex. For instance, there are 8 species or subspecies of *Artemisia* that dominate various plant communities. Three juniper and 2 pinyon species occur in different portions of the ecoregion.

METHODS FOR A REGIONAL GAP ANALYSIS

The first critical issue in mapping land cover is selecting a classification system that is ecologically defensible and yet feasible for mapping at a regional scale with remote sensing and limited field information. The alliance level of the proposed National Vegetation Classification System (NVCS; Federal Geographic Data Committee 1996) was selected as the most appropriate schema. Derived from the UNESCO system (UNESCO 1973, Driscoll et al. 1984), this hierarchical scheme begins with structural and broad ecological properties at higher levels, adding floristic divisions at lower levels. Alliances are named by their dominant canopy species within structural classes based on life-form and canopy closure. Proposed NVCS standards define closed tree canopy (i.e., forest) as tree cover of 60–100%, open tree canopy or woodland with 25–60% tree cover, shrubland classes with >25% shrub cover and <25% tree cover, and herbaceous classes with <25% shrub or tree cover. An example of an alliance in the ISD ecoregion would be the *Pinus ponderosa* alliance within the rounded-crowned temperate or subpolar needle-leaved evergreen open canopy tree formation. Because the same dominant species also occurs within a closed canopy tree formation, there are 2 *P. ponderosa* alliances distinguished by canopy closure. For simplicity, we use the terms *forest* and *woodland* in the text in place of the closed and open canopy terminology when referring to land-cover classes.

Land cover was originally mapped independently for each of the states in the ISD ecoregion (Kagan and Caicco 1992, Caicco et al. 1995, Davis et al. 1995, Driese et al. 1997, Homer et al. 1997, Cassidy in press). Although most state GAP projects used 1990 (±2 yr) satellite imagery from the Landsat Thematic Mapper (TM) sensor, combined with field inventories and existing maps of vegetation in compiling their land-cover data, they differed in methods and products. Maps for Idaho (Caicco et al. 1995) and Oregon (Kagan and Caicco 1992) used photointerpretation techniques with older, lower-resolution Multispectral Scanner (MSS) images and had larger minimum mapping units than the other states. In contrast, land-cover mapping in Nevada and Utah was done with digital image processing of TM image mosaics (Homer et al. 1997). This approach generally achieved greater spatial resolution at some expense in classification detail. The other state projects fall somewhere in between these methods, using manual photointerpretation of higher resolution TM data (e.g., Davis et al. 1995, Driese et al. 1997, Cassidy in press). Few maps have been validated with a formal accuracy assessment (except see Caicco et al. 1995, Edwards et al. 1995).

For this ecoregional analysis, a regional land-cover map was required but with greater spatial and thematic consistency than was contained in the collection of state-level maps. Therefore an innovative technique was developed to utilize the state GAP maps as training data and then reclassify satellite data into a common set of NVCS cover types. First, all land-cover classes in the state GAP maps were converted to alliances as prescribed by the NVCS. In some cases it was necessary to aggregate to a higher level where dominant species could not be distinguished in related alliances (e.g., deciduous riparian forest types). Pixels of multi-temporal satellite imagery from the NOAA Advanced Very High Resolution Radiometer were then assigned to these cover types using a maximum likelihood classifier. Some cover types that were either rare or occur in small patches were not classified with the 1-km^2 satellite data but were retained from the original maps. Thus, the final map had a consistent spatial resolution (1-km^2 or 100-ha pixel size) across the entire ISD ecoregion while retaining the best floristic information from the original maps (Stoms et al. in press).

Although a comprehensive map accuracy assessment of the regional land-cover map has not been undertaken, the map was compared to a set of randomly distributed 1-km^2 field plots compiled nationwide by the U.S. Forest Service (Zhu et al. 1996). Seventy-eight of these plots occur within the ISD ecoregion. This small sample size is insufficient for a statistical per-class assessment but adequate for a preliminary indication of the strengths and weaknesses of the land-cover map. Each plot record listed dominant tree and/or shrub species and their relative canopy cover, total absolute tree cover in classes similar to the NVCS definitions of open and closed canopy, presence of grasses (identified as annuals or perennials), and presence of agriculture. Based on species composition and cover, each plot was assigned to one (or in some cases to a set) of the cover types in the regional land-cover map.

Maps of land-stewardship and land-management status were also compiled for individual state gap analysis projects, usually by digitizing BLM Surface Management Status maps. Maps of special managed areas were compiled from a wide variety of sources (see Caicco et al. 1995 and Davis et al. 1995 for details). These maps were combined to create a regional map. GAP uses a scale of 1–4 to denote relative degree of maintenance of biodiversity for each tract of land. A status of 1 denotes the highest, most permanent level of maintenance, and 4 represents the lowest level of biodiversity management as evidenced by legal and institutional factors. Each tract of land is assigned to 1 of the 4 status levels as defined by Scott et al. (1993):

Status 1: An area having permanent protection from conversion of natural land cover and a mandated management plan in operation to maintain a natural state within which disturbance events (of natural type, frequency, and intensity) are allowed to proceed without interference or are mimicked through management. Included are Research Natural Areas, many wilderness areas, national parks and monuments, and Nature Conservancy preserves.

Status 2: An area having permanent protection from conversion of natural land cover and a mandated management plan in operation to maintain a primarily natural state, but which may receive use or management practices that degrade the quality of existing natural communities. Most National Wildlife Refuges, Areas of Critical Environmental Concern, and some state parks are included in this category.

Status 3: An area having permanent protection from conversion of natural land cover for the majority of the area, but subject to extractive uses of either a broad, low-intensity type or localized intense type. It also confers protection to federally listed endangered and threatened species throughout the area. Undesignated public lands managed by the U.S. Forest Service or the BLM are examples of this status category.

Status 4: Lack of legally enforced easement or mandate to prevent conversion of natural habitat types to anthropogenic habitat types. Allows for intensive use throughout the tract. Also includes those tracts for which sufficient information to establish a higher status is not available. Privately owned lands (except for private conservation group reserves), most Department of Defense tracts, and state school lands are included in this category.

Intersecting the land-stewardship and management map with the distribution of land-cover classes results in tables that summarize the area and percent of total mapped distribution of each class in different land-stewardship and management categories. The percentage and acreages of cover types in each management status category and managed by each steward were quantified (Caicco et al. 1995).

RESULTS

Land Cover and Alliances

Forty-eight land-cover classes were mapped for the region (Table 1), including 2 cultural land-use types, 5 nonvegetated or sparsely vegetated types, 16 formations or undifferentiated groups of related alliances, and 25 alliances. Formations tend to be relatively scarce types that occur in small patches or as linear features. For instance, the seasonally/temporarily flooded cold-deciduous forest formation consists of alliances dominated by *Populus tremuloides*, *P. fremontii*, *P. balsamifera*, *P. angustifolia*, or other riparian tree species. At the regional scale it was not feasible to discriminate between them. Species of pinyon and juniper have overlapping range (except *Juniperus occidentalis*, which has a distinct geographic range), and so were grouped into 3 more general classes. Similarly, 2 *Cercocarpus* classes (*C. ledifolius* and *C. montanus*) that occur in the ecoregion could not be distinguished in the land-cover mapping. Mixes of canopy species with no clear dominants were also mapped at the formation level. This

TABLE 1. Percentage of mapped area of land-cover classes by management status in the Intermountain Semi-Desert ecoregion. Formation names shown in bold italics.

Land-cover class	Status 1 (%)	Status 2 (%)	Status 3 (%)	Status 4 (%)	Total area (km²)	% of ecoregion
Rounded-crowned temperate or subpolar needle-leaved evergreen closed tree canopy						
Pinus contorta forest	14.1	4.1	72.9	8.9	2,726	0.7
Pinus ponderosa forest	0.0	3.6	42.4	54.0	106	<0.1
Pinus ponderosa–Pseudotsuga menziesii forest	0.0	0.4	47.4	52.2	1,350	0.3
Conical-crowned temperate or subpolar needle-leaved evergreen closed tree canopy						
Abies species (*A. concolor, A. grandis,* or *A. magnifica*) forest or woodland	0.0	2.3	51.4	46.3	183	<0.1
Picea engelmannii and/or *Abies lasiocarpa* forest or woodland	5.9	0.2	71.3	22.5	606	0.1
Pseudotsuga menziesii forest	1.4	1.2	63.8	33.5	3,335	0.8
Montane or boreal cold-deciduous closed tree canopy						
Populus tremuloides forest	5.6	4.4	59.6	30.4	1,038	0.3
Seasonally/temporarily flooded cold-deciduous closed tree canopy						
Populus fremontii, P. balsamifera, P. angustifolia, P. tremuloides, Salix, Alnus, Betula, etc.	2.5	11.9	14.1	71.5	1,053	0.3
Rounded-crowned temperate or subpolar needle-leaved evergreen open tree canopy						
Pinyon woodland (*Pinus edulis* or *P. monophylla*)	0.0	0.1	52.6	47.3	332	0.1
Pinyon-juniper woodland (*Pinus edulis* or *P. monophylla* with *Juniperus osteosperma* or *J. scopulorum*)	11.1	0.0	51.1	37.7	391	0.1
Juniper woodland (*Juniperus osteosperma* or *J. scopulorum*)	0.2	3.8	57.1	38.9	6,728	1.6
Juniperus occidentalis woodland	1.1	2.0	51.0	46.0	17,609	4.3
Pinus flexilis or *P. albicaulis* woodland	7.2	0.5	44.6	47.7	1,141	0.3
Pinus contorta woodland	13.8	7.2	52.2	26.8	373	0.1
Pinus jeffreyi forest and woodland	0.0	0.0	68.0	32.0	181	<0.1
Pinus ponderosa woodland	0.1	3.0	37.9	59.0	7,599	1.9
Conical-crowned temperate or subpolar needle-leaved evergreen open tree canopy						
Pseudotsuga menziesii woodland	0.9	0.2	70.6	28.3	706	0.2
Cold-deciduous open tree canopy						
Populus tremuloides woodland	1.3	1.9	50.4	46.3	1,896	0.5
Quercus garryana woodland	0.0	3.0	13.7	83.3	643	0.2
Microphyllous evergreen shrubland						
Artemisia tridentata ssp. *vaseyana* shrubland	0.8	2.6	50.5	46.0	24,702	6.0
Artemisia tridentata–A. arbuscula shrubland	0.6	4.8	68.7	26.0	46,047	11.2
Artemisia tridentata shrubland	1.1	2.9	63.7	32.3	117,263	28.6
Artemisia tripartita shrubland	0.0	1.4	29.4	69.1	3,494	0.9
Purshia tridentata shrubland	0.0	0.3	29.9	69.8	1,071	0.3

aggregation occurred for cover classes such as mountain brush in the temperate cold-deciduous shrub formation, mixed salt desert shrub primarily composed of various *Atriplex* species, and grassland types. Grasses were divided into dry (e.g., *Pseudoroegneria* and *Poa* spp.) and moist (e.g., *Festuca* spp.) perennial bunchgrass, an annual grassland (primarily the exotic *Bromus tectorum*), and artificial seedings of *Agropyron cristatum* or *Poa pratensis*. One alliance is defined by a subspecies—mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*), where it could be mapped separately from other *A. tridentata* subspecies.

Three land-use or land-cover types account for 57% of the region—*Artemisia tridentata* (29%), agriculture (17%), and *A. tridentata–A. arbuscula* (11%). Other significant types include *Juniperus occidentalis* (4%), *A. tridentata* ssp. *vaseyana* (6%), mixed salt desert shrub (6%),

TABLE 1. Continued.

Land-cover class	Status 1 (%)	Status 2 (%)	Status 3 (%)	Status 4 (%)	Total area (km²)	% of ecoregion
Temperate cold-deciduous shrubland						
Artemisia cana shrubland	14.3	0.9	59.8	25.0	532	0.1
Mountain brush shrubland	3.5	1.9	49.3	45.3	3,339	0.8
Cercocarpus ledifolius or *C. montanus* shrubland	1.0	1.2	50.7	47.2	1,136	0.3
Quercus gambelii shrubland	0.0	0.1	17.6	82.2	379	0.1
Seasonally/temporarily flooded cold-deciduous shrubland	2.0	10.0	43.0	45.0	2,568	0.6
Extremely xeromorphic deciduous subdesert shrubland with or without succulents						
Sarcobatus vermiculatus shrubland	0.8	5.2	51.9	42.1	5,996	1.5
Facultatively deciduous extremely xeromorphic subdesert shrubland						
Mixed salt desert shrub (*Atriplex* spp.)	0.6	1.0	66.2	32.1	22,668	5.5
Dwarf-shrubland						
Artemisia nova dwarf-shrubland	0.0	3.9	66.9	29.3	573	0.1
Artemisia arbuscula–A. nova dwarf-shrubland	0.0	8.4	76.5	15.1	1,813	0.4
Artemisia rigida dwarf-shrubland	0.3	0.2	38.2	61.2	881	0.2
Atriplex gardneri dwarf-shrubland	0.0	1.0	79.5	19.4	9,898	2.4
Temperate or subpolar perennial grassland						
Dry grassland–*Pseudoroegneria* (*Agropyron*)–*Poa*	0.2	4.3	18.9	76.5	21,222	5.2
Moist grassland–*Festuca*	0.0	3.1	7.8	89.1	1,927	0.5
Temperate or subpolar perennial grassland–cultivated						
Agropyron cristatum seedings, *Poa pratensis*, hayfields, and Conservation Reserve Program lands	0.2	0.7	68.5	30.5	8,267	2.0
Temperate or subpolar annual grasslands or forb vegetation						
Annual grasses–*Bromus tectorum*, etc.	0.7	0.6	50.5	48.2	11,522	2.8
Non-tidal temperate or subpolar hydromorphic rooted vegetation (marsh and wetland)	0.2	38.0	7.2	54.6	518	0.1
Alpine and subalpine meadows of the higher latitudes						
Alpine tundra	0.0	0.0	100.0	0.0	3	<0.1
Wet or dry meadow	34.7	4.0	43.1	18.1	177	<0.1
Sparsely vegetated land-cover types						
Seasonally/temporarily flooded sand flats	0.0	0.2	73.3	26.5	2,341	0.6
Sparsely vegetated sand dunes	0.9	26.4	47.6	25.2	851	0.2
Sparsely vegetated boulder, gravel, cobble, talus rock	0.2	3.4	64.9	31.5	2,415	0.6
Cultural land use types and surface water						
Urban or human settlements and mining					1,684	0.4
Agriculture					64,473	15.7
Open water, including ponds					2,220	0.5
Regional totals (including cultural land uses and surface water)	**0.9**	**2.8**	**49.5**	**46.9**	**411,277**	

and annual grassland (5%). Seventeen types had mapped distributions of <1000 km² each (or 0.25% of the regional area).

The land-cover map and Forest Service field plots showed general agreement. Thirty-one (40%) of the plots were completely consistent with the land-cover map in both structural and floristic attributes. Another 17 (22%) plots were at least partially consistent, such as where the same species were recorded but percent canopy cover in the plot would assign them to a different formation type than the map did. The largest discrepancies tended to be between grassland and sparse shrub cover, in part because it is difficult with satellite data to discriminate accurately the 25% shrub cover threshold on a continuous gradient from grass to shrub. Several state maps had a sagebrush-steppe class that was always assigned to an *Artemisia tridentata* alliance at the regional level, even though in some cases the shrub cover might be <25%. Another 15 (19%) of the plots that disagreed with the map were located within 1 pixel's width (1 km) of a landscape with the correct type according to the plot, which could be attributed to a combination of map registration error, mixed pixels at ecotones, and more generally to the fuzziness of transitions between alliances. Absolutely wrong labels, according to the plots, were assigned to 13 (17%) samples. We emphasize that this comparison is only indicative of the strengths and weaknesses of the land-cover map but, due to the small sample size, conveys no statistical significance about its accuracy.

Land Stewardship and Management Status

Sixty percent of the land in the ISD ecoregion is publicly owned (Table 2). The steward with the greatest holdings is the Bureau of Land Management (45.4% of the total land area). The U.S. Forest Service and state governments control slightly more than 4% each. Tribal lands account for 2.8% of the region, while the U.S. Fish and Wildlife Service, Department of Energy, Department of Defense, Bureau of Reclamation, National Park Service, and county or regional governments make up the remainder of public lands in descending order of area. Private lands, including a very small proportion of nongovernmental organization holdings, constitute nearly 40%.

Greater than 96% of the ecoregion is managed such that extractive resource uses are permitted and biodiversity conservation is not a primary objective (status 3 and 4, Table 2). Only 0.9% (3648 km^2) is designated to be maintained in its natural state by formal designation (status 1), with an additional 2.8% (11,288 km^2) managed as status 2 lands (Fig. 2). The Bureau of Land Management, U.S. Fish and Wildlife Service, Department of Energy, and state lands constitute the major stewards of this protected land. This regional pattern of small proportions of status 1 and 2 with approximately equal amounts of status 3 and 4 is repeated in both subregions (Table 3). The Wyoming Basin has slightly more public land but less formally protected land than the Columbia Plateau subregion.

If the status 1 and 2 managed areas are examined without regard to steward or site name but are simply aggregated into disjunct spatial units, there are 809 separate sites with a median size of just 252 ha (mean size of 1886 ha). Of these, 228 are <100 ha in size, and another 399 are between 100 and 500 ha. Despite the large number of small sites (78% of the total number), they account for only 7% of the area of all status 1 and 2 lands. Only 26 sites are >10,000 ha, but represent >70% of protected area. Five managed areas are each >50,000 ha—Sheldon National Antelope Range (>220,000 ha) in northwestern Nevada, Idaho National Environmental Engineering Lab, Hart Mountain National Antelope Range in Oregon, Owyhee River Bighorn Sheep Habitat Area of Critical Environmental Concern (ACEC) managed by the Bureau of Land Management in Idaho, and Malheur National Wildlife Refuge–Steens Mountain ACEC complex in Oregon.

Gap Analysis of Land-cover Classes

The profile of management status for each land-cover type for the ISD ecoregion is shown in Table 1. This table can be summarized by categorizing the percentage of total area of each type within status 1 and 2 managed areas. Categories include types not represented in any status 1 or 2 managed area, types with ≤1%, 1–10%, 10–20%, 20–50%, and >50%. The number of land-cover types in each category for the region and for each subregion is shown in Table 4. Despite the low level of representation across most types, the representation is an unbiased sample of the communities of the ISD ecoregion (chi square = 52.57, 43 df, P = 0.849). That is, the pattern of representation across types is not significantly different than if sites had been selected with the intention of achieving equal representation for all cover types.

TYPES WITH NO REPRESENTATION IN STATUS 1 AND 2 MANAGED AREAS.—Only 2 natural land-cover types are completely unrepresented within the ISD ecoregion according to the regional maps: *Pinus jeffreyi* and alpine tundra. Similarly, several cover types are not represented in status 1 and 2 lands within 1 of the 2 subregions, even though they are represented within the ecoregion as a whole. These

TABLE 2. Percentage of land by management status by steward in the Intermountain Semi-Desert ecoregion.

Steward	Status 1 (%)	Status 2 (%)	Status 3 (%)	Status 4 (%)	Area (km²)	Area (%)
Private, including NGOs	0.1	0.5	0.1	99.4	163,005	39.6
County/regional government	0.0	0.0	100.0	0.0	2	~0.0
State government	0.1	7.4	19.4	73.1	19,381	4.7
Bureau of Land Management	0.5	1.7	97.8	0.0	186,663	45.4
National Park Service	73.5	26.5	0.0	0.0	317	0.1
U.S. Fish and Wildlife Service	29.8	68.8	1.4	0.0	4,581	1.1
U.S. Forest Service	5.2	0.2	94.6	0.0	16,857	4.1
Tribal lands	0.0	0.0	0.0	100.0	11,488	2.8
Department of Energy	0.0	69.9	0.0	30.1	3,441	0.8
Bureau of Reclamation	7.7	2.0	0.0	90.3	1,160	0.3
Military reservations / Corps of Engineers	0.0	0.2	0.0	99.8	2,161	0.5
Large water bodies	—	—	—	—	2,220	0.5
ISD ecoregion total	0.9	2.8	49.5	46.9	411,277	100.0

TABLE 3. Percentage of land by management status by subregion in the Intermountain Semi-Desert ecoregion (does not include water bodies).

Subregion	Status 1 (%)	Status 2 (%)	Status 3 (%)	Status 4 (%)	Area (km²)
Wyoming Basin	0.6	1.3	55.3	42.8	118,942
Columbia Plateau	1.0	3.5	47.0	48.5	290,617
ISD ecoregion total	0.9	2.8	49.5	46.9	409,559

TABLE 4. The number of land-cover classes at various percentage levels of representation in existing managed areas (status level 1 and 2 combined). Does not include open water, *Agropyron cristatum* seedings, or cultural land-cover types.

Subregion	# not represented	# with ≤1%	# with 1–10%	# with 10–20%	# with 20–50%	# with >50%	Total #
Wyoming Basin	4	7	14	2	4	0	31
Columbia Plateau	4	7	20	5	5	1	42
ISD ecoregion total	2	7	26	5	4	0	44

unrepresented types in the Columbia Plateau include the *Pinus ponderosa* forest and *P. contorta* woodland alliances. In the Wyoming Basin unrepresented types are pinyon-juniper woodland, mountain brush, *Cercocarpus ledifolius* or *C. montanus*, and *Purshia tridentata*.

TYPES WITH ≤1% IN STATUS 1 AND 2.—Seven alliances or cover types have minimal representation (<1% of their mapped extent) within the ISD ecoregion. These include *Pinus ponderosa–Pseudotsuga menziesii* forest, pinyon woodland, *Purshia tridentata*, *Quercus gambelii*, *Artemisia rigida*, *Atriplex gardneri*, and seasonally/temporarily flooded sand flats (alkali playa). Minimally represented types in one of the subregions, in addition to those listed for the ISD ecoregion, are *Pseudotsuga menziesii* woodland and *A. nova* in the Columbia Plateau and *Pinus flexilis* or *P. albicaulis* woodland and dry perennial grassland in the Wyoming Basin subregion.

TYPES WITH 1–10% IN STATUS 1 AND 2.—Twenty-six types are in this category, including the most widespread ones such as the various *Juniperus* and *Artemisia tridentata* types, *Sarcobatus vermiculatus* and mixed salt desert shrub, dry grassland, and annual grassland. The *Artemisia tridentata–A. arbuscula* shrubland type has proportions by status level that are nearly identical to the region as a whole (Fig. 3).

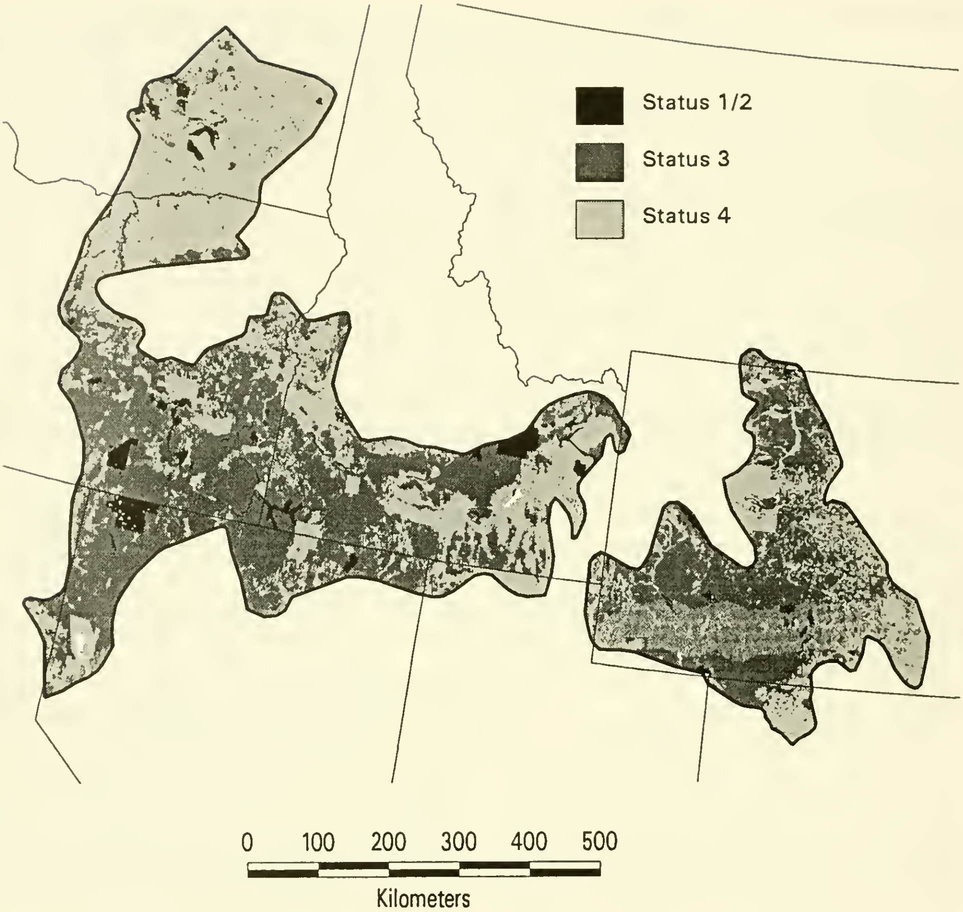

Fig. 2. Land-management status of the Intermountain Semi-Desert ecoregion (levels are defined in the text).

TYPES WITH 10–20% IN STATUS 1 AND 2.—Five alliances or cover types have this level of representation in the ecoregion. These types are the *Pinus contorta* forest alliance, seasonally/temporarily flooded cold-deciduous (i.e., riparian) forest, pinyon-juniper woodland, *Artemisia cana* shrubland, and seasonally/temporarily flooded cold-deciduous shrubland.

TYPES WITH 20–50% IN STATUS 1 AND 2.—Four types are in this category—the *Pinus contorta* woodland alliance, non-tidal or subpolar hydromorphic rooted vegetation (i.e., marsh and wetland), wet or dry alpine or subalpine meadows, and sparsely vegetated sand dunes. In addition to these types, the seasonally/temporarily flooded cold-deciduous forest and shrubland types have this level of representation in the Columbia Plateau subregion. The *P. contorta* forest alliance is similarly represented in the Wyoming Basin.

TYPES WITH >50% IN STATUS 1 AND 2.—There are no types in this category in the ecoregion. Only the *Pinus flexilis* or *P. albicaulis* woodland type has 67% representation in the Columbia Plateau subregion, while the Wyoming Basin has none.

DISCUSSION

Limitations of Regional Gap Analysis

Gap analysis at the state or regional scale is subject to limitations pertaining to its basic assumptions and those related to technological limitations and ecological realities of mapping a specific study area. We address both forms

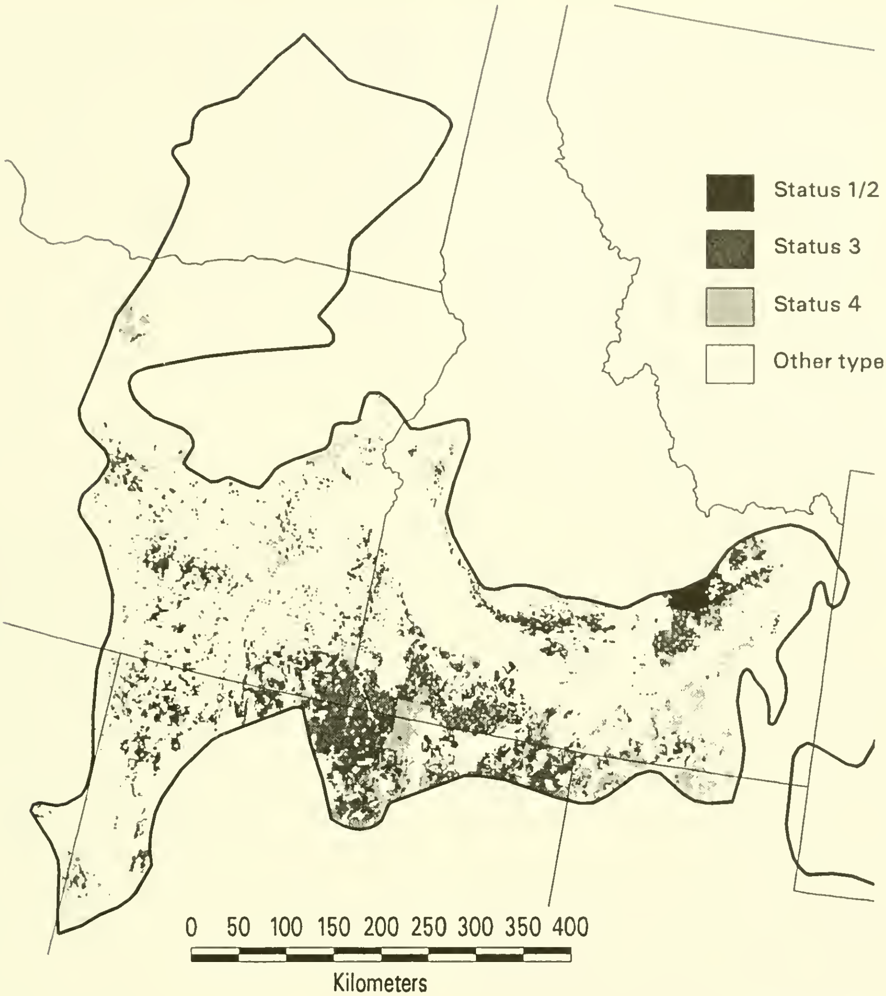

Fig. 3. Land-management status of the *Artemisia tridentata–A. arbuscula* shrubland type in the Intermountain Semi-Desert ecoregion (levels are defined in the text).

here. Gap analysis is defined as an expanded coarse-filter approach to conservation (Scott et al. 1993). It provides a baseline assessment of the distribution and management of biodiversity elements at a given point in time. As such, it attempts to characterize the variability of biodiversity across large geographic regions with moderately low-resolution map information. This rapid assessment requires the use of satellite remote sensing data, supplemented with a modest amount of field observation and any existing land-cover maps. Some plant communities frequently occur in patches below the 100-ha minimum mapping unit of the current mapping phase of gap analysis and consequently may be omitted from or underestimated in the regional analysis. Their omission highlights the need for complementary fine-filter assessments at more local scales to investigate a more complete range of biodiversity in a region. As a baseline assessment, gap analysis provides little or no information on current conditions or past trends in the community. Where changes in disturbance regime such as the increase in fire frequency have caused a conversion from sagebrush to dense annual grasses, the land-cover map depicts the current grassland type, but the loss of the original cover type is undocumented. Impacts from grazing or other activities that change the quality of the cover type but not its classification are not portrayed.

A similar limitation of gap analysis is its underlying assumption that land-management status is determined by the intentions expressed by the steward in formal designations or agency mission statements, not the actual or permitted land uses on specific tracts which tend to be more difficult to ascertain. For example, public lands may be inaccessible or otherwise not suitable for intensive resources uses and be de facto wilderness areas. GAP normally assigns these lands to status 3, however, because digital map information on site-specific management is not widely available and future use is uncertain. Most lands under stewardship of the Department of Defense are categorized as status 4 (except for such dedicated sites as Research Natural Areas) because there is no permanent protection offered for biodiversity. Management may change with the needs of the national defense or with reassignments of base commanders. Some tracts of Department of Defense lands, however, are relatively undisturbed compared to some other public lands. As regional-scale data on land uses and other threats to biodiversity become more widely available in electronic form in the future, the vulnerability of communities could be more directly assessed than by using land-management classes as a surrogate for threats. In the meantime, this is the best approximation.

To test the validity of this assumption, we compared the GAP land-status map with a map of categories of impact of permitted land uses on natural ecological processes compiled for the Interior Columbia Basin assessment area (Quigley et al. 1996). For the geographic area of overlap, there was very close correspondence between the status classifications based on designation and those based on permitted uses (Table 5). GAP status levels 1 and 2 areas were primarily managed for maintaining natural ecological processes. Only 3% of these lands allowed intensive uses. Over 80% of status 3 lands managed by the BLM and the USFS were being managed for a variety of ecological and human needs, most often with high levels of activity and vegetation manipulation. Roughly 15% of the area in status level 3 was also being managed for natural ecological processes and conservation of representative or rare biodiversity elements. Thus, 16,000 km^2 of undesignated public land is managed in ways compatible with designated GAP status 1 and 2. The premise of GAP, however, is that without the assurance of formal designation, the protection offered in current management plans cannot be considered long term. Such areas currently managed for low-intensity uses could, however, be designated with only minor economic impacts. It should be noted that the Interior Columbia Basin assessment area does not cover the entire ISD ecoregion, and management category data were compiled for only BLM and USFS lands. The findings of this comparison of management classifications cannot necessarily be extended to private or to other public lands.

TABLE 5. Correspondence of GAP status levels based on designation with management categories from the Interior Columbia Basin Ecosystem Management Project (ICBEMP) based on actual and planned land uses on national forest and Bureau of Land Management lands. The ICBEMP categories are summarized as follows: 1 = natural ecological processes, 2 = non-intensive human uses in conservation areas, 3–4 = low-intensity human uses in balance with ecological integrity, 5–6 = vegetation manipulation for resource use, 7–8 = ecological conditions significantly altered by human activities.

GAP status level	ICBEMP management categories				
	1	2	3–4	5–6	7–8
1	82.8	9.9	4.6	2.8	0.0
2	60.4	20.3	10.9	7.8	0.7
3	14.2	0.8	4.2	79.2	1.6

Despite general consensus among ecologists and conservation planners that conservation assessments should be conducted over ecologically and biogeographically meaningful regions, there has been no universally accepted system for mapping ecoregions suitable for all purposes. We chose the ECOMAP mapping of regions (Bailey 1995) because it is in wide use throughout the Forest Service for ecosystem management and forms the basis for regional planning by other groups (The Nature Conservancy Ecoregional Working Group 1996). It is not clear how different our biological assessment might have been if a different regionalization had been selected. In general, cover types in the 2 subregions had similar management status, suggesting that relatively minor boundary adjustments would probably have little effect on the identification of conservation gaps. Where atypical plant communities are present only near the boundary of the region, we have not highlighted them as high conservation priority. No matter what ecoregion scheme one chooses, the distribution of some communities will span more than a single region. There may be biologically important variation within such communities that is reflected by ecoregional boundaries. If one's goal is to capture the full range of biological variation of a type within special management areas, it may be prudent to assess its status across its entire range. One such approach is to assess representation by latitudinal, longitudinal, and elevational variables which have been found to vary with biotic composition and ecological processes (Mike Scott personal communication).

The land-cover map of the ISD ecoregion contains several limitations in classification that affect the findings of this analysis to an unknown degree. Aside from those related to the omission of fine-grain patches of communities, the greatest source of uncertainty relates to canopy closure in assigning vegetation to formations. Source maps were not consistent in how (or whether) forest and woodland were discriminated. Consequently, identification of tree-dominated formations in the NVCS hierarchy is probably less reliable than dominant canopy species information. Tree-dominated cover types, however, are minor components of the vegetation of the ecoregion and occur primarily at the margins. The accuracy of the separation of grassland from shrubland along the continuous gradient of increasing shrub density is also uncertain in the land-cover map. The greatest uncertainty between alliances occurs among various sagebrush species and subspecies, which were not always distinguished in the source maps. To some extent these were identified in the regional land-cover map with elevation data. The final point to emphasize is that some cover types could not be meaningfully assigned to an alliance, such as where the vegetation has no clear dominant species. As an example, mountain brush is an aggregate class representing a mixture of deciduous shrub species. No species dominates this type and the mix of dominant species varies between locations, so no alliance named for a dominant species was practical. In other cases the difficulty lies with the NVCS schema. Where individual alliances are all rare and closely related (e.g., seasonally/temporarily flooded cold-deciduous forest), it was necessary to aggregate to the formation level. Thus, the quantitative findings should be considered as preliminary indications of potential gaps in the coarse-filter representation of plant communities.

Management Implications of the Gap Analysis

With these limitations in mind, we draw on other published literature to interpret the raw numbers provided by the analysis. On the basis of level of representation in status 1 and 2 areas, the degree to which land-cover types are characteristic of the ISD ecoregion, and the extent of historic loss or degradation of habitat or modification of disturbance regime, we have tentatively categorized land-cover types by relative priority for conservation attention. Higher-priority categories are listed in Table 6. States in which more than 20% of the mapped distribution occurs, and stewards who manage at least this amount, are also shown in Table 6 to alert principal stakeholders of planning and management responsibilities.

Highest priority types have minimal biodiversity protection and are vulnerable to expected land-use activities; their extent and management status may be crudely estimated at the scale of regional mapping. Seasonally/temporarily flooded cold-deciduous forest and shrubland types generally occur in narrow linear strips adjacent to rivers and streams, while marshes and meadows tend to be quite small. These patterns make them difficult to map comprehensively. Further, they contain many different alliances consisting of a variety of dominant species, and so the status of individual riparian alliances is unknown. Riparian types depend on flood scouring for germination, which has frequently been prevented by dams (Noss et al. 1995). Thus, simply allocating nature reserves without other management actions aimed at maintaining ecological processes will not preserve them. Further, these 4 types are sensitive to disturbance and valuable for wildlife habitat. Native perennial bunchgrasses are poorly represented in status 1 or 2 lands (both types at <5%) and have been substantially modified by introduced annual grasses or converted to agriculture. Three-fourths of Küchler's fescue/wheatgrass (*Festuca/Pseudoroegneria* spp.) potential natural vegetation type in eastern Washington has been

TABLE 6. States where the most vulnerable land-cover classes primarily occur (>20% of the distribution of the type in status 3 and 4) and stewards most responsible for their management (>20% in status 3 and 4). States and stewards listed in descending order of extent, if more than one is listed. * indicates rare type that may be underestimated, so other states and stewards may be involved as mapping is refined.

Land-cover class	States	Stewards
FIRST-PRIORITY CLASSES		
Seasonally/temporarily flooded cold-deciduous forest	WY *	Pvt *
Seasonally/temporarily flooded cold-deciduous shrubland	WY, ID *	BLM, Pvt *
Dry grassland–*Pseudoroegneria* (*Agropyron*)–*Poa*	WA, WY, OR	Pvt
Moist grassland–*Festuca*	OR, WA	Pvt
Non-tidal temperate or subpolar hydromorphic rooted vegetation (marsh and wetland)	ID, OR, WA *	Pvt *
Wet or dry meadow	WY, UT *	FS, Pvt *
Sparsely vegetated sand dunes	WY *	BLM, Pvt *
SECOND-PRIORITY CLASSES		
Artemisia tridentata ssp. *vaseyana* shrubland	ID, WY, NV	BLM, Pvt
Artemisia tridentata–*A. arbuscula* shrubland	ID, NV, OR	BLM, Pvt
Artemisia tridentata shrubland	WY, OR	BLM, Pvt
Artemisia tripartita shrubland	WA	Pvt, BLM
Purshia tridentata shrubland	OR	Pvt, BLM
Artemisia cana shrubland	OR	BLM, Pvt
Sarcobatus vermiculatus shrubland	WY, OR	BLM, Pvt
Mixed salt desert shrub (*Atriplex* spp.)	WY, NV	BLM, Pvt
Artemisia nova dwarf-shrubland	WY, OR	BLM, Pvt
Artemisia arbuscula–*A. nova* shrubland	ID	BLM
Artemisia rigida dwarf-shrubland	OR *	Pvt, BLM *
Atriplex gardneri dwarf-shrubland	WY	BLM
Seasonally/temporarily flooded sand flats	NV	BLM, Pvt
THIRD-PRIORITY CLASSES		
Juniper woodland (*Juniperus osteosperma* or *J. scopulorum*) woodland	WY, ID	BLM, Pvt
Juniperus occidentalis woodland	OR	BLM, Pvt
Populus tremuloides forest	OR, WY, NV	BLM, FS, Pvt
Populus tremuloides woodland	WY, CO	Pvt, FS, BLM
Mountain brush	ID	Pvt, BLM, FS
Cercocarpus ledifolius or *C. montanus* shrubland	WY, OR	BLM, Pvt
Sparsely vegetated boulder, gravel, cobble, talus rock	WY	BLM, Pvt

converted to other land uses while the wheatgrass/bluegrass (*Pseudoroegneria/Poa* spp.) type has lost 31% of its presettlement extent (Klopatek et al. 1979). Both perennial grassland types are predominantly on privately owned lands (dry = 77%, moist = 89%). It will take a combination of preservation and active management to maintain adequate representation of the bunchgrass types. Sparsely vegetated sand dunes may also be underestimated because dunes beneath sparse vegetation cover are difficult to recognize in satellite images. Management must protect dune-forming processes to preserve the dune community and should also recognize that many plants are endemic to specific dunes. Despite a moderately high level of representation in status 1 and 2 areas, this cover type needs a fine-filter investigation to ensure protection of the individual plant species it represents. BLM wilderness study areas in Wyoming could substantially increase the proportion of status 1 for this type (Merrill et al. 1996).

Second priority includes types where their current biodiversity protection is minimal, types are characteristic of the ecoregion, and they are vulnerable to expected land-use activities. Klopatek et al. (1979) reported a 15% loss of sagebrush steppe to other land uses, largely agriculture. Locally, the impact on sagebrush steppe has been much more severe, such as a substantial conversion of big sagebrush habitat in the Snake River plain (Noss et al. 1995). Only 1% of the sagebrush steppe has been unaffected by livestock grazing, with 30% being heavily grazed (West 1996). The major impact of grazing has been a decrease in perennial bunchgrasses with a corresponding increase in woody shrub cover. The introduction of *Bromus tectorum* has increased fire frequency in many locations to the extent that annual grasses have totally supplanted sagebrush (West 1988). Because of the selective grazing pressure on palatable species, even lightly grazed areas cannot be fully restored to a pristine condition (West 1996). Public agencies have responded to the removal of native herbs through heavy grazing by seeding large areas with introduced *Agropyron cristatum* (crested wheatgrass). Restoring these degraded or seeded sagebrush steppe sites would be extremely expensive and possibly beyond our current understanding (West 1996). The *Artemisia tripartita* and *Purshia tridentata* alliances are noteworthy because they both have 70% of their mapped distributions on private lands. In contrast, 2/3 of the *A. nova* type occurs on public lands. The actual management status of *A. rigida* (stiff sagebrush) dwarf shrubland, with 61% in status 4, is only an estimate. It was not mapped in Idaho where it is known to occur on small patches of specific soils that were below the resolution of the original Idaho land-cover map (Caicco et al. 1995).

The xeric cover types, including mixed salt desert shrub, *Atriplex gardneri* (which was mapped only in the Wyoming Basin subregion but does occur in the Columbia Plateau), *Sarcobatus vermiculatus*, and seasonally/temporarily flooded sand flats, are also in the second-priority category. These types tend to be arranged in distinct gradients of moisture and alkalinity in valley bottoms, with strong competitive sorting of species. Stutz (1978) proposes that rapid evolutionary divergence and hybridization within the *Atriplex* genus may be occurring in different valleys in Wyoming, Nevada, and Utah. If true, this would argue for protection of many replicates in this ecoregion and in the Intermountain Semi-Desert and Desert ecoregion to the south to nurture this evolutionary process. Currently, <2% of the mixed salt desert shrub type is in status 1 or 2 lands. The seasonally/temporarily flooded sand flats, or alkali playa, type is even less well represented at 0.2%. The *A. gardneri* and *S. vermiculatus* alliances have 1% and 6% representation, respectively, but are not highly vulnerable to grazing impacts because of the defense mechanisms of their dominant species. Over 80% of the *A. gardneri* type was mapped on public lands, primarily under the jurisdiction of the BLM. Formally designating the BLM wilderness study areas in the state of Wyoming, however, would contribute very little additional protection for these 4 desert types (Merrill et al. 1996).

Third-priority land-cover types are those that have low representation in existing biodiversity management areas but do not appear highly vulnerable from the kinds of activities that are most probable. Also included are types which have complex, highly variable floristic composition. These types require further study to assess their conservation status in greater detail, perhaps with finer separation of alliances within the type. *Juniperus occidentalis* has doubled in areal extent, at least in Idaho and Oregon, where it has replaced sagebrush steppe communities as a result of fire suppression (Miller and Rose 1995) and reduced herbaceous fuel in the understory from heavy livestock grazing (West 1988). Given that juniper woodlands are expanding into sagebrush steppe, management concern lies more with the fire regime than necessarily increasing their representation in designated managed areas. *Populus tremuloides* forest and woodland are also dependent on periodic disturbance. Mountain brush within the ISD ecoregion is at the northern limits of its range (Caicco et al. 1995). It is perhaps one of the most complex classes in the ecoregion with a diverse mix of canopy shrubs that can vary dramatically between sites. This floristic complexity makes mountain brush a difficult class about which to draw meaningful conclusions concerning its protection status with GAP data, so it needs to be examined in greater detail. The *Cercocarpus* alliance tends to occur on steep, rocky outcrops which are not prone to development. In fact, as a fire-sensitive species, *Cercocarpus* has expanded its range since the beginning of fire suppression (Kagan and Caicco 1992). While not of the highest conservation priority, it should still receive further consideration (Merrill et al. 1996). The sparsely vegetated boulder, gravel, cobble, and talus rock is a very general class for many types of essentially bare ground. Little can be concluded about its biodiversity value except at a more site-specific scale.

Fourth priority includes types that tend to be marginal to the ISD ecoregion. These types may be of concern but are better assessed in neighboring regions or across their entire range. These types include all conifer forest and woodland types (except juniper woodlands), *Quercus garryana* woodland, *Q. gambelii* shrubland, and alpine tundra. The gap analysis projects in Idaho and Wyoming in combination provide some of that broader perspective for a few of the types marginal to the ISD ecoregion. *Pinus contorta* forest and woodland types are more characteristic of the northern Rocky Mountains where they also appear to be well represented (Caicco et al. 1995, Merrill et al. 1996). *P. flexilis* occurs mostly in the Wyoming Basin on sites unsuitable for most human land uses. Even though it is not well protected by formal land-management designations, it is not highly vulnerable and not a high conservation priority in the ecoregion (Merrill et al. 1996). The *Picea engelmannii* and/or *A. lasiocarpa* forest and woodland type is widespread throughout the mountains of Idaho and Wyoming where it is well represented (approximately 40% in each state) in status 1 and 2 lands (Caicco et al. 1995, Merrill et al. 1996).

CONCLUSIONS

A gap analysis was conducted for the Intermountain Semi-Desert ecoregion using data compiled from 9 states. Despite limitations in the data, our gap analysis provides the first systematic assessment across all ownerships of the management status of plant communities within a multistate region. Forty-eight land-cover types were mapped at the regional level, many of which are at the alliance level of classification. Twenty types were determined to be the highest conservation priorities, as they are especially vulnerable to future losses or degradation in the absence of formal designation or active intervention for long-term biodiversity management. Over 96% of the terrestrial environment within the region is potentially available to intensive human uses for resources, recreation, or urbanization; the proportions are similar for the Columbia Plateau and Wyoming Basin subregions. We urge that findings regarding individual vegetation types from this assessment be carefully validated by regional field investigation to better determine their true level of representation and actual vulnerability to threats before policy decisions are made and implemented.

One of the motivations for conducting gap analysis for an ecoregion rather than for political jurisdictions is to reflect more accurately the vulnerability of communities over their ranges. Findings from a sample of the community, such as a single state, could be misleading and generate inefficient conservation action. Generally, land-cover types had similar management status in the ISD ecoregion analysis as they did in the 3 gap analyses published to date for Idaho (Caicco et al. 1995), Utah (Edwards et al. 1995), and Wyoming (Merrill et al. 1996). Types with low representation within individual states were likewise poorly represented in the region. Well-represented types at the state level were mostly conifer forest types that occur in Yellowstone National Park and large wilderness areas of central Idaho, which are outside the ecoregion. Thus, even if these tree-dominated types had low representation in the ISD ecoregion, we felt they were not a high conservation priority regionally. This correspondence of state and regional findings in this particular instance is probably not typical.

Beyond the initial conservation assessment, these findings can be applied in at least 2 additional directions. First, they can provide a regional perspective when the impacts of specific land-use proposals are investigated. GAP data can quantify how rare a community type is, where else it occurs, and how well it is represented in biodiversity management areas. Second, the data from GAP can play a significant role in follow-up conservation planning efforts at a statewide or regional level (Crowe 1996, Vickerman 1996). For instance, GAP data such as shown in Figure 3 can provide the missing biodiversity dimension in discussions about alternative wilderness and national park proposals (Wright et al. 1994, Merrill et al. 1995, 1996, Wright and Scott 1996). The Nature Conservancy has already used the GAP database from the Columbia Plateau subregion as a coarse-filter to identify candidate areas to ensure adequate representation of all community types. Because GAP projects are now underway in almost every state in the nation, data to support other regional analyses and conservation planning will soon be forthcoming.

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NATURAL HISTORY OF A SALINE MOUND ECOSYSTEM

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ABSTRACT.—Along the margins of playas in northwestern Nevada, a salt-tolerant plant community occupies mounds that dot a largely unvegetated landscape. In this environment we studied soil development and plant-soil relationships. The mounds, averaging 0.3 m in height, are occupied by the shrubs *Allenrolfea occidentalis* (iodine bush), *Sarcobatus vermiculatus* (black greasewood), and *Atriplex lentiformis* ssp. *torreyi* (Torrey saltbush). *Distichlis spicata* (desert saltgrass) is the only herbaceous plant occupying this community. Soil salinity decreases with depth in this environment, and content of aqueous-extractable solutes is significantly influenced by site-specific vegetation. Content of silt, clay, and salt in mound surface horizons suggests a chronosequence of mound formation, with the youngest at the barren playa interface and the oldest at the upland vegetation border. Plant demography and mound soil stratigraphy suggest that a pulse of plant recruitment and mound building occurred during a time of neoglacial cooling. As a substrate for plant recruitment, mounds have a limited lifespan because deposition of eolian-transported salts and geochemical cycling by plants quickly render them too saline for seed germination. The apparent periodicity of mound formation precludes definitive conclusions regarding those mound characteristics favorable for plant recruitment and survivorship.

Key words: Allenrolfea occidentalis, Atriplex lentiformis *spp.* torreyi, *eolian dust,* Sarcobatus vermiculatus.

Vegetated mounds, hummocks, or hillocks occur in desert climates worldwide (Shantz and Piemeisel 1940, Bendali et al. 1990, Danin 1991). The origin of these features is generally thought to be capture of eolian sediment by vegetation (Gile 1966, Vasek and Lund 1980), thus the term pythogenic hillock (Batanouny and Batanouny 1968). Plants occupying these mounds often have adaptive growth characteristics such as aerial structures and roots and runners favoring the capture and stabilization of eolian materials (Bendali et al. 1990). Colonization of mounds by cryptogamic organisms lends further stability to the soil (Danin 1991).

During the Pleistocene the Lahontan Basin of northwestern Nevada consisted of numerous interconnected lakes (Russell 1885). At the onset of the Holocene, these pluvial lakes receded leaving a complex of highly saline, fine-textured lacustrine sediments intermixed with coarser-textured, less saline, deltaic, beach, and offshore bar deposits. Fluviatile sands and eolian-reworked material offered a favorable substrate for plant colonization culminating in the presently diverse plant community (Young et al. 1986).

Post-pluvial recruitment on the very saline playa sediments, however, was problematic. Neal and Motts (1967) suggested that plant recruitment on playas may hinge on the formation of large desiccation cracks. These cracks accumulate sediment, presumably of low osmotic potential, capture seeds, have higher available water content for establishing seedlings, and begin the process of mound building. Another pathway of plant recruitment on saline playas occurs when phreatophytic species are able to tap into low osmotic potential groundwater and then begin mound building (Neal and Motts 1967). Assumed in the previous recruitment process is a favorable establishment phase sufficiently long to allow plant roots to reach the water table; this process likely hinges on optimal climatic conditions and a high water table. Jacobson and Jankowski (1989) present another mechanism for plant recruitment on saline playas. At discharge spots, evaporative concentration establishes dense brine pools. Crystallization of gypsum in capillary zones heaves the ground, which can then be colonized by halophytic plants.

Research was initiated to understand plant-soil relationships and the history of mound development in this arid, saline environment. Two basic questions were asked: (1) Is mound formation a prerequisite to the establishment and evolution of plant communities? (2) Conversely, are mounds happenstance, a natural consequence of aerodynamic baffling by vegetation in an environment with a high flux of wind-transported material? Working hypotheses developed during initial fieldwork postulated that the principal pedogenic processes operating were eolian dust capture by vegetation to form mounds, and that new mounds form in upland positions while mounds closest to the barren playa are eroding.

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METHODS

The study was conducted in Eagle Valley (39°44′N, 119°2′W), 64 km east-northeast of Reno, Nevada. Eagle Valley is a small embayment of pluvial Lake Lahontan bounded to the northwest by the Truckee Range and to the southeast by the Hot Springs Mountains. The western boundary of the playa was the terminus of the Truckee River during pluvial periods and consists of coarse-textured deltaic and reworked eolian sands. Elevation of the barren playa surface in the study area is 1234 m. At maximum lake levels during pluvial cycles of the Pleistocene (Morrison 1964), water covered Eagle Valley to a depth of approximately 100 m. Presently, water ponds on the barren playa surface only during years of heavy runoff. Our principal study area is at the eastern end of the playa (Sec. 26, T22N, R26E). The location is a gradient from barren, flat, fine-textured, salt-encrusted sediments to a higher, coarser-textured, and less saline complex of reworked beach material, eolian sands, and alluvial colluvial material emanating from Hot Springs Mountains. This transitional area where halophytic plant communities exist on mounds is the focus of this study (Fig. 1). Nearby Fallon, Nevada (elevation 1209 m), with average precipitation of 12.5 cm yr^{-1}, had the following precipitation (cm) during the study period: 1988 = 12.9, 1989 = 12.2, 1990 = 14.5, 1991 = 8.3, 1992 = 10.4, 1993 = 14.0, 1994 = 13.3. Based on data from monitor wells installed throughout the study area, the water table is <3 m in most years. Mounds are dominated by *Allenrolfea occidentalis* ([S. Watson] Kuntze), *Atriplex lentiformis* ssp. *torreyi* ([S. Watson] H.M. Hall & Clements), and *Sarcobatus vermiculatus* ([Hook.] Torrey) and by the grass *Distichlis spicata* ([L.] Greene) (Young et al. 1986). In the less saline and coarse-textured beach and colluvial deposits, vegetation is dominated by *Atriplex confertifolia* and *Sarcobatus baileyi* (Billings 1945).

Six mounds, each supporting *A. occidentalis*, *S. vermiculatus*, *A. lentiformis* ssp. *torreyi*, and *D. spicata*, were randomly selected in 1989. From each mound we collected soil samples beneath each individual plant microsite (approximately 10 cm deep excluding the surface crust). We also collected composite soil samples from (1) barren mound surfaces, to 10 cm, (2) the surface 10 cm of lacustrine material beneath the mound centers, and (3) interdune sediment immediately adjacent to the mounds, 0–10 cm. A saturation extract was prepared for each soil sample (U.S. Salinity Laboratory Staff 1954). Electrical conductivity was measured with a salinity drop tester. Ion chromatography was used to quantify Na^+, K^+, Cl^-, NO_3^-, and SO_4^{-2}.

To explore the spatial distribution patterns of soluble salts in mound environments, we randomly selected 3 mounds in 1990. A grid pattern was overlain on the mounds. At nodes of the grid, we collected a 7.6-cm-diameter core to the depth at which lacustrine sediments were encountered or to 30 cm, whichever was shallower; the surface crust was excluded. Samples were placed in bags, brought to the laboratory, air-dried, and stored until analyzed. Extraction of soluble species was facilitated by placing 10 g of the homogenized original sample in 50-mL centrifuge tubes, adding 10 mL deionized water, and shaking for 1 h. The tubes were centrifuged and subsamples tested for electrical conductivity with a salinity drop tester and for pH with a glass electrode. Other subsamples were diluted with deionized water to appropriate levels for analyses by the ion chromatograph for Cl^-, Br^-, NO_3^-, SO_4^{-2}, Na^+, K^+, Mg^{+2}, and Ca^{+2}. Boron was determined using the azomethine-H colorimetric procedure (John et al. 1975). For one of the mounds, particle size analysis was done as described below. The spatial distribution of each individual attribute is presented in an XYZ contour fill chart facilitated by a commercial graphics program.

In 1990 we described a sequence of 7 soils along a transect encompassing the width of the mounded area from the barren playa surface southeast to the less saline upland interface (transect distance ≈ 1.2 km). A backhoe was used to excavate to a depth of approximately 3 m. Soils were described using established

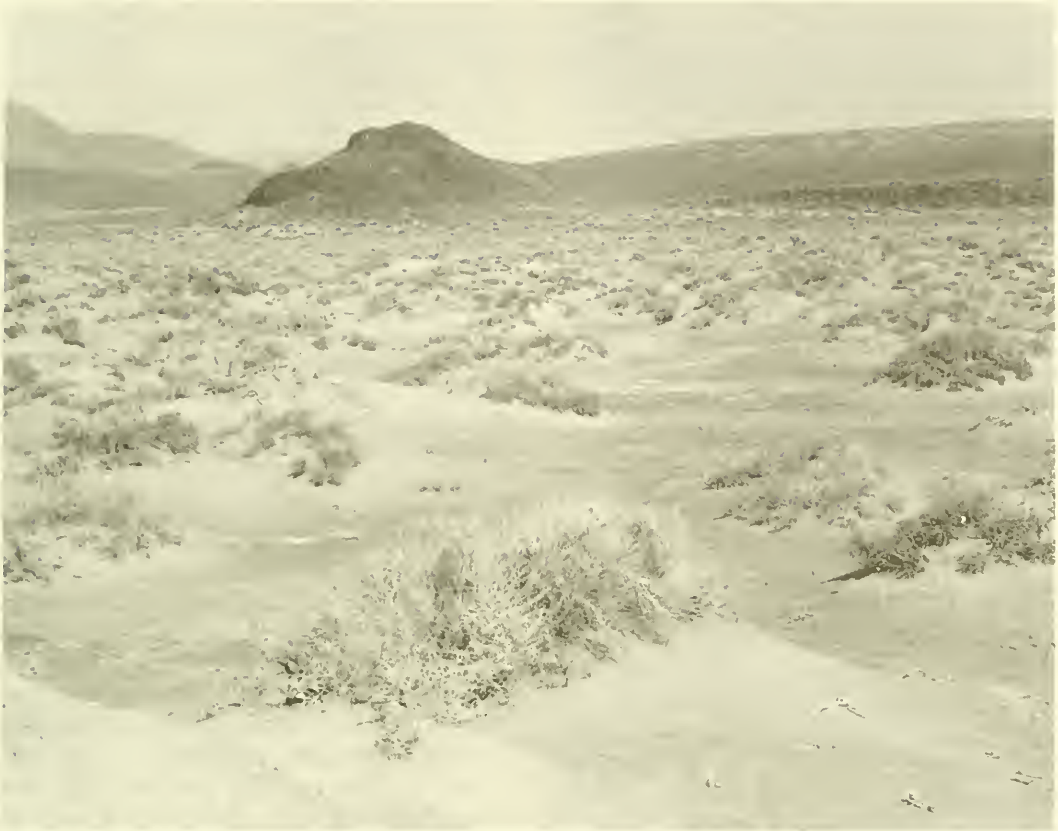

Fig. 1. Landscape photograph of study areas showing mounds occupied by *Allenrolfea occidentalis*. For 50 mounds measured, the average length was 3.1 m (s = 1.8), average width was 1.9 (s = 1.1), and average height was 0.3 m.

protocols (Soil Survey Staff 1984). Samples of each horizon were returned to the laboratory for further characterization. We quantified the following attributes: (1) organic carbon by the dichromate digestion procedure (Nelson and Sommers 1982); (2) particle-size distribution after removal of organic matter and soluble salts (Gee and Bauder 1986); (3) saturated paste extraction (U.S. Salinity Laboratory Staff 1954) with quantification of anions and cations by ion chromatography. Clay-sized fractions reserved from particle-size analyses were prepared for and examined by X-ray diffraction using standard procedures (Moore and Reynolds 1989). The very fine sand fraction was examined with a petrographic microscope to identify its mineralogy (Brewer 1976). The silt-sized fraction was isolated by dry-sieving of original samples and examined by X-ray diffraction.

At approximately 1-mon intervals in 1991, we collected soil samples at depths of 20, 40, and 60 cm from 4 randomly selected mounds. After transport to the laboratory in sealed glass vials on ice, the samples were immediately analyzed for gravimetric water content and total soil water potential (Decagon SC-10 thermocouple psychrometer). Calibration of the psychrometer was facilitated using saturated salt solutions of LiCl (–294.4 MPa), NaCl (–38.0 MPa), KCl (–21.7 MPa), and KNO_3 (–7.5 MPa), and NaCl solutions with potentials of –3.2 MPa and –1.8 MPa.

To quantify eolian dust fluxes and chemical content, we placed marble dust collectors (3 replicates) on the barren playa surface approximately 8 km southwest of the study area. The marble dust collectors consisted of approximately a 5-cm depth of glass marbles placed in 33 × 24-cm teflon-coated cake pans placed on the soil surface. Collectors were sampled bimonthly from June 1994 through June 1995, at which time dust weight was recorded. A subsample of the dust was dissolved in deionized water (1-g sample 25 mL H_2O) and analyzed for Cl^-, NO_3^-, SO_4^{-2}, Na^+, and K^+ using ion chromatography and for Boron using the azomethine-H colorimetric procedure.

RESULTS

Soils

Except for the soil described on a large dune (soil 5), soils along the transect have grossly similar morphology and stratigraphy even between mound and intermound microsites (Table 1). Vesicular surface crusts overlying soft, sandy loam layers are common to all soils. Hues are 2.5Y in surface layers grading to 5Y in lower layers (Munsell color system). A textural discontinuity exists in all soils examined: sandy loam surface layers overlie silty clay loam varved lacustrine sediments. The upper several centimeters of the lacustrine unit contain many indurate nodules ranging from 1 to 5 cm in diameter. Tubular pores are abundant in the finer-textured material. These pores are in places peripherally coated by what appears to be organic material, perhaps old root channels. The proportion of sand in surface horizons decreases from the barren playa surface to the higher portion of the landscape at soil 7; silt and clay content correspondingly increases. In excavated sections of mounds, graded-bedding and cross-bedding were evident in the surface coarse-textured material.

Organic carbon levels are very erratic among soil horizons (Table 1). There is a slight increase in organic carbon in the lower mottled, reduced horizons. Organic carbon is highest in the surface crust of soil 7. Visual inspection of this layer did not show any evidence of rooting activity, but the crust had encased seeds and fruits of halophytic species that occupy the mounds.

Saturation paste extracts show the extreme salinity of this environment (Table 1). Complete solubilization of some salts may not have occurred for some samples given the soil-to-water ratios used. These systems are dominated by Na^+ and Cl^-. Levels of Na^+ and Cl^-, as well as other solutes, generally decline with depth. Extractable SO_4^{-2} values are erratic among soils and among soil horizons. Soils on the lowest part of the landscape (1, 2, 3, and 4) have a secondary bulge in profile SO_4^{-2} levels, which is absent in soils 5, 6, and 7. Levels of K^+ are inconsistent among soils and among horizons. Levels of NO_3^- are extraordinarily high in the surface crust of all soils, generally declining rapidly with depth.

Clay-sized mineralogy is similar among the soils examined. In the coarse-textured material overlying varved lacustrine materials, K-saturated treatments produce reflections corresponding to lattice spacings for kaolin, mica, and a poorly crystalline, randomly interstratified smectite-illite. With Mg^{+2} saturation and glycol intercalation, the randomly interstratified component expands to 1.6 nm with very broad reflections. Lacustrine sediments are dominated by smectite. One unusual X-ray trace was for the 5th layer of soil 3, the horizon with anomalously low pH (Table 1). The pattern was completely amorphous save for a very broad maximum centered at 0.40 nm, which is indicative of opaline silica (Jones and Segnit 1971).

X-ray diffraction was used to examine the silt-sized mineralogy of soils 1, 3, and 6. Samples were dry-sieved from original material to conserve water-soluble minerals. A peak matching algorithm was used to detect minerals in the samples. The principal evaporite mineral identified in the silt-fraction was halite (NaCl), which occurred in all soil layers above the lacustrine sediments. The only other evaporite mineral identified was bloedite ($Na_2MgSO_4 \cdot 4H_2O$), which occurred in layer 1 of soil 3. Other principal minerals in all horizons in decreasing order of abundance were plagioclase feldspar, quartz, calcite, and mica. Gypsum ($CaSO_4 \cdot 2H_2O$) was a major mineral component in layers 4 and 5 of soil 3 and the surface horizon of soil 5, both vegetated. Diagnostic peaks for sepiolite (ideal = $Si_{12}Mg_8O_{30}(OH)_4(OH_2)_4 \cdot 8H_2O$) were found in the 5th layer of soil 1. No zeolites were identified in the silt fraction even though saline playa environments are known to foster their formation (Ming and Mumpton 1989).

Mineralogy of the very fine sand fraction was determined by optical methods and quantified using the line count method (Brewer 1976). Samples were washed with water to remove soluble salts. The mineralogy of soil above lacustrine sediments is dominated by plagioclase feldspar and quartz with minor volcanic glass, hornblendes, mica, and carbonates. Much of the lacustrine material consisted of diatom tests partially or completely cemented by an isotropic material that appears to be silica.

Plant-Soil Relationships

The content of aqueous extractable solutes varied significantly among collection microsites (Fig. 2). The most saline microsites were unvegetated areas atop mounds and the soil beneath greasewood. Soil collected in the unvegetated zone adjacent to mounds and the playa material directly beneath the mounds had in general the lowest levels of extractable solutes among the collection microsites.

Using a backhoe, we were able to uncover a root system of *A. occidentalis* that emanated from a mound and extended over 10 m into the unvegetated interspace. The directionality of the root systems suggests linkages among mounds, although we did not excavate a complete root system from one mound to another. The diameter of larger roots was over 5 cm. Most large-diameter roots had over 90 growth rings, the oldest having 120 rings. Soil-water relations data collected in 1991, a wetter than normal year, show the extremely negative total soil water potentials characteristic of this environment (Table 2).

Soil samples from 3 spatially separated mounds were collected in a grid pattern to determine the spatial distribution of aqueous-soluble solutes. Canopy coverage of the mounds by *A. occidentalis* ranged from approximately 1/2 (Fig. 3a) to much less than 1/2 occupied (Fig. 3c). Spatial distribution of aqueous-soluble solutes differs considerably among the 3 mounds. There is a correspondence between levels of aqueous-soluble solutes and location of plant canopies for mounds a and b. In mound a the highest electrical conductivity and K^+ occur beneath *S. vermiculatus* plants; for mound c, levels of Mg^{+2} and SO_4^{-2} are especially high beneath *A. occidentalis* plants on the south side of the mound. Mound b, which has the greatest canopy coverage by *A. occidentalis*, generally has the lowest solute concentration near the top of the mound corresponding roughly to a nonvegetated area. There is also a directional aspect of solute distribution. Many solutes are highest in the southwest quadrant (all mounds). Coarse sand content shows a gradient from north to south (mound a). Very fine sand content is highest at the top of the mound, and silt and clay are highest at mound edges (mound a).

Eolian Dust

The bimonthly eolian dust flux on the barren playa surface averages over 130 g m^{-2} (Table 3). The dust is dominantly composed of Na^+ and Cl^- (nearly 40% by weight) with very high levels of water-soluble SO_4^{-2}, K^+, and NO_3^-. Concentration of phytotoxic boron averages over 1400 mg kg^{-1}.

DISCUSSION

Mound Pedogenesis

Particle-size distribution indicates that soil development began on a surface that was relatively coarse textured in comparison to the underlying lacustrine material. Depositional fabrics such as cross- and graded-bedding and the areal extent of the coarse-textured veneer suggest it is a remnant offshore bar likely reworked by beach and wind action as the pluvial lake receded. Thus, mounds are a composite of eolian material overlying offshore beach deposits.

In the Lake Lahontan basin, given geomorphic surface stability, the proportion of fines (silt and clay) increases with time via the steady capture of eolian dust in the soil skeletal framework of sand- and gravel-sized particles (Chadwick and Davis 1990). In our study the proportion of fines in mound surface layers increases from the barren playa interface to the surrounding upland. Based on the Chadwick and Davis model, youngest mounds are closest to the barren playa, which is supported by mound stratigraphy. Mounds closest to the barren playa show greater relief and have more visual evidence of recent eolian sand deposition. Moreover, as expected, there is a general increase in mound salinity from the playa to the upland because, as time increases, cumulative additions of salt-rich eolian dust (Table 4) and plant geochemical cycling of salts also increase (Robert 1950, Charley and West 1977). Expansion of vegetated mounds into barren playa surfaces is opposite the general conclusion that playas in western United States have generally enlarged during the Holocene (Blackwelder 1931, Malek et al. 1990). However, Eagle Valley may be unique due to the immense volume of coarse-textured deltaic sediments generally upwind of the study area (prevailing winter storm winds from the northwest).

The controlling factors of pedogenesis in this environment are eolian erosion and deposition,

TABLE 1. Soil descriptions and selected attributes by horizon.

Horizon	Depth (cm)	Munsell color (dry)	Roots	Effervescence HCl	pH	OC (%)	Size distribution			Saturated paste					Field notes
							Sand	Silt	Clay	Na^+	Cl^-	SO_4^{-2}	K^+	NO_3^-	
							%			mM					
BARREN PLAYA SURFACE—SOIL 1, approximately 200 m southwest of Eagle Rock															
C1	0–8	2.5Y 7/2	absent	slight	7.4	0.42	77.6	14.9	7.5	3480	3410	46.4	20.1	1.40	surface salt efflorescences
Bk1	8–30	2.5Y 7/2	absent	violent	7.3	0.36	62.8	26.3	10.9	2670	2550	20.8	16.1	0.27	platy structure
Bk2	30–51	2.5Y 6/2	absent	strong	7.2	0.45	44.5	30.1	25.4	2540	2490	20.2	23.8	0.21	platy structure
C2	51–64	2.5Y 7/2	absent	slight	7.3	0.44	48.1	30.4	21.5	1870	2360	20.4	21.6	0.26	many vesicles and tubular pores
2Cg1	64–91	5Y 5.5/3	absent	slight	7.4	0.72	2.5	44.4	53.1	1460	1630	34.0	36.7	0.12	varved: streaks of 2.5YR 6/8; pyrite coatings
2Cg2	91+	5Y 5.5/3	absent	slight	7.4	0.82	3.9	45.7	50.4	2810	1540	17.2	28.3	0.03	extremely hard when dry; mottles of 5YR 7/8
ALLENROLFEA MOUND—SOIL 2, approximately 200 m southeast of soil 1															
A	0–8	2.5Y 6.5/2	absent	slight	7.9	0.43	73.3	12.8	13.8	2810	2620	82.5	21.1	0.44	stolons of *Distichlis spicata*
C1	8–23	2.5Y 6.5/2	common	strong	8.1	0.30	83.0	5.8	11.1	380	420	34.9	7.7	5.78	roots concentrated at bottom of horizon
Bk	23–56	2.5Y 7/2	few	violent	8.2	0.17	65.0	18.7	16.3	400	410	6.2	3.8	0.07	forms granules when dry that easily pulverize
Cc	56–91	5Y 7/2	v. few	strong	8.2	0.13	54.3	26.3	19.4	220	200	3.0	4.9	0.17	strong local cementation
C2	91–127	5Y 7/2	v. few	strong	8.2	0.21	62.4	20.4	17.2	210	220	11.0	3.4	0.83	
2Cg	127+	5Y 8/0	v. few	strong	8.0	0.47	7.8	45.4	46.8	220	250	3.5	7.6	nd	pyrite coatings
ALLENROLFEA-SARCOBATUS MOUND—SOIL 3, 12 m south of soil 2															
A	0–1.5	2.5Y 6/3	absent	strong	7.8	0.32	78.8	7.1	14.1	990	960	33.0	7.3	6.61	slightly hard surface crust; vesicular porosity
C1	1.5–20	2.5Y 6.5/2	common	strong	8.1	0.20	75.6	12.6	11.7	540	550	12.7	5.9	0.05	pulverizes easily
C2	20–76	2.5Y 6.5/2	few	strong	8.3	0.65	85.7	5.8	8.5	310	300	43.1	4.6	0.49	very soft
By	76–86	2.5Y 6/2	v. few	strong	8.0	0.21	nd	nd	nd	270	280	41.6	4.0	0.08	gypsum crystals; seams of calcium carbonate
C3	86–122	5Y 6/3	common	none	5.2	0.74	68.0	16.0	16.0	380	410	12.3	3.4	0.01	decaying root debris
2C	122–157	2.5Y 7/2	v. few	strong	8.0	0.20	48.2	28.0	23.8	160	170	16.5	2.6	0.11	pulverizes easily; many tubular pores
2Cg	157+	2.5Y 7.8/2	v. few	violent	8.1	0.45	8.1	54.9	37.0	120	140	6.5	3.2	0.02	varved structure; black coatings of pyrite
UNVEGETATED INTERSPACE—SOIL 4, approximately 350 m southeast of soil 3															
A	0–2.5	2.5Y 6.5/2	absent	strong	7.8	0.65	69.5	15.0	15.5	3710	3860	56.6	14.9	7.70	surface crust; vesicular porosity
Bk	2.5–30	2.5Y 6.5/2	v. few	violent	7.9	0.22	69.1	14.1	16.7	630	650	3.0	9.5	0.09	very soft

TABLE 1. Continued.

Horizon	Depth (cm)	Munsell color (dry)	Roots	Effervescence HCl	pH	OC (%)	Size distribution			Saturated paste					Field notes
							Sand	Silt	Clay	Na⁺	Cl⁻	SO_4^{-2}	K⁺	NO_3^-	
							%			mM					
UNVEGETATED INTERSPACE—SOIL 4, approximately 350 m southeast of soil 3															
C1	30–51	5Y 6.5/2	few	strong	8.1	0.31	37.5	35.1	27.4	330	330	1.8	4.3	0.08	pulverizes easily
C2	51–64	2.5Y 7/2	few	violent	7.6	0.30	44.8	27.3	27.9	1070	1130	37.4	13.1	0.58	many tubular pores
2Cc	64–81	2.5Y 6.5/2	v. few	violent	8.0	0.40	18.5	51.7	29.8	170	190	1.7	3.4	0.03	strong local cementation
2C	81–112	5Y 7/2	v. few	strong	8.3	0.58	nd	nd	nd	110	150	2.9	3.1	0.03	strong fine blocky structure
2Cg	112+	5Y 8/2	v. few	slight	8.2	0.49	1.4	56.3	42.4	100	130	1.1	7.0	0.01	varved structure; few black pyrite coatings
VEGETATED LARGE DUNE—SOIL 5, approximately 50 m east of soil 4															
A	0–2.5	2.5Y 7/2	absent	strong	7.9	0.39	61.4	16.0	22.5	2480	2240	210.4	12.1	0.32	gypsum crystals
C1	2.5–15	2.5Y 6.5/2	few	strong	7.7	0.33	74.4	5.4	20.2	3770	3800	177.6	11.0	8.51	graded bedding
C2	15–43	2.5Y 6/2	few	strong	8.2	0.15	76.8	9.7	13.6	830	780	86.2	7.3	2.52	graded bedding
C3	43–76	2.5Y 6/2	few	moderate	8.0	0.11	77.7	7.5	14.7	230	190	68.3	1.5	0.11	graded bedding
C4	76–132	2.5Y 6/2	v. few	slight	8.0	0.10	81.6	6.8	11.6	110	110	52.3	1.2	0.14	graded bedding
2Bt	132+	10YR 6/3	v. few	slight	8.2	0.10	71.0	16.7	12.3	80	110	6.9	1.7	0.20	common clay films
UNVEGETATED INTERSPACE —SOIL 6, approximately 280 m southeast of soil 4															
A	0–5	2.5Y 6/2	absent	strong	7.5	0.57	53.7	24.2	22.1	4010	4150	48.0	14.1	1.23	surface crust; vesicular porosity
C1	5–10	2.5Y 6/2	absent	strong	7.9	0.46	47.3	29.0	23.7	1760	1460	28.2	12.8	0.30	shiny ped faces
C2	10–33	2.5Y 6.5/2	few	violent	8.2	0.20	60.3	21.6	18.1	490	460	7.9	4.0	0.04	many tubular pores
C3	33–51	5Y 8/1.5	v. few	violent	7.6	0.47	9.0	56.1	34.9	720	730	5.2	12.7	0.05	many tubular pores
2Cc	51–69	5Y 8/1	v. few	strong	7.7	0.52	3.6	49.9	46.4	640	660	4.4	16.3	0.08	strong local cementation; many tubular pores
2C	69–99	5Y 8/2	v. few	strong	7.8	0.43	3.5	47.4	49.0	310	330	2.1	8.4	0.08	varved structure; many tubular pores
2Cg	99–127	5Y 7/3	v. few	slight	7.7	0.38	5.5	50.8	43.7	190	220	1.7	5.1	0.07	black pyrite coatings; many tubular pores
2Cg2	127+	5Y 7/3	v. few	slight	7.6	0.38	4.4	49.4	46.1	210	250	2.6	5.8	0.03	coating of rustlike 5.0 YR 5/6
ALLENROLFEA MOUND—SOIL 7, approximately 400 m south of soil 6															
A	0–8	2.5Y 7/2	absent	violent	7.0	1.03	46.9	31.4	21.7	4630	5550	20.3	18.8	4.17	puffy surface crust; vesicular porosity
2C1	8–13	2.5Y 7/2	v. few	strong	8.0	0.87	12.2	60.9	26.8	2510	2520	15.8	46.3	4.70	pulverizes easily
2C2	13–46	2.5Y 7/2	v. few	strong	7.5	0.60	11.2	60.9	27.9	1130	1360	5.0	22.4	1.41	pulverizes easily
2C3	46–86	2.5Y 8/2	v. few	strong	7.8	0.46	5.5	56.0	38.5	450	450	1.0	12.2	0.08	strong, fine, angular blocky structure
2Cg1	86–112	5Y 8/1.5	v. few	strong	8.1	0.38	12.3	49.0	38.7	80	120	0.9	2.3	0.03	hard when dry; many tubular pores
2Cg2	112+	5Y 8/1.5	v. few	strong	8.1	0.49	6.2	48.7	45.0	150	170	1.0	6.0	0.05	a few pyrite coatings; many tubular pores

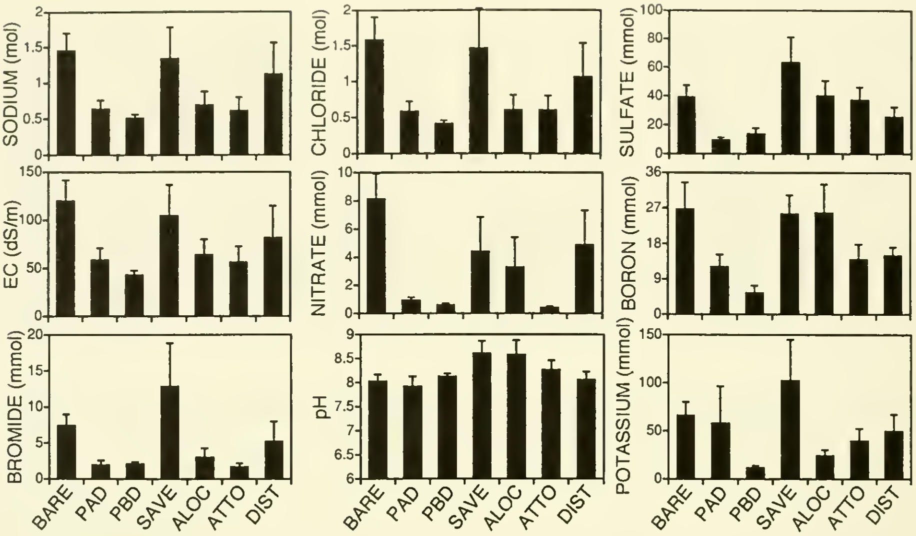

Fig. 2. Aqueous extractable solutes as influenced by collection microsite. Codes are as follows: BARE = top of mound with no vegetation; PAD = surface soil of unvegetated mound interspace; PBD = lacustrine sediment beneath mound; SAVE, ALOC, ATTO, and DISP = collected beneath *S. vermiculatus*, *A. occidentalis*, *A. torreyi*, and *D. spicata*, respectively. Values are means ±1 $s_{\bar{x}}$.

extreme aridity, high salinity, halophytic vegetation, and aeration status of the lower lacustrine sediments. Erosion and deposition via wind action are a constant in these salt desert environments (Young and Evans 1986). The magnitude of eolian transport in the study area is immense (Table 3). Moreover, deposition of dust in obstructions such as plant canopies would rapidly increase their salt content to levels too high for future seedling recruitment. The situation thus exists where eolian materials both build the vegetated mounds and are also partially responsible for their demise at some later date due to excessive salt accumulation and eventual plant death. As will be discussed later, we are not sure mound building is contemporaneous with steady salt accumulation from dust, or whether the mound-building phase requires some different climate from that present when less saline, coarser-textured eolian dust is more plentiful.

The study area's scant precipitation precludes extensive leaching of solutes through the soil. Steady additions of salt-rich eolian dust and plant deposition of salts on the soil surface appear to quickly make mounds extremely saline.

One of the consequences of extremely high salt content in soils is the accelerated physical breakdown of sand-sized particles to silt-sized particles by salt weathering (Goudie et al. 1970). In addition, the high salt content in conjunction with aridity and plant processes leads to extreme alkalinization such as seen in *S. vermiculatus* microsites (Robertson 1983). The locally high pH condition enhances the weathering of primary minerals via increased solubility of aluminum, iron, and silicon (Loughnan 1969).

At present, plant factors come into play only on the mounds themselves. One plant pedogenic aspect is the biogeochemical concentration of elements that accelerates mound salinization due to the capture of eolian dust alone. The yearly fall of leaves and seeds becomes incorporated, enriching the mound surface horizon with organic matter. Vegetation seems to play a role in the formation of gypsum, as only vegetated mounds contain measurable quantities. Gypsum formation may be a function of plant concentration of calcium and sulfur in mound soil to such levels that gypsum can precipitate. Alternatively, mound microclimate may foster the crystallization of gypsum via salt exclusion from ice (Marion and Grant 1997).

Another factor in the genesis of these soils is the extremely reduced nature of the lacustrine sediments as indicated by gley soil colors, mottling, and the presence of pyrite (FeS)

TABLE 2. Water relations, by depth, of mounds (values are means with standard errors in parentheses; $n = 4$).

Date	Gravimetric water content by depth (cm)			Total soil water potential by depth (cm)		
	20	40	60	20	40	60
	%			MPa		
5/30/91	13.2 (6.5)	20.9 (6.5)	24.8 (5.4)	–22.7 (3.7)	–11.2 (3.2)	–8.3 (2.2)
6/10/91	13.7 (6.0)	26.5 (13.0)	27.1 (5.9)	–15.2 (3.4)	–12.7 (5.1)	–5.2 (0.8)
7/8/91	9.4 (5.1)	27.6 (10.3)	23.1 (11.1)	–14.6 (4.3)	–6.8 (1.5)	–6.3 (1.3)
8/30/91	5.0 (1.4)	23.9 (10.6)	28.7 (7.3)	–22.1 (2.7)	–8.0 (1.8)	–8.0 (2.1)
9/30/91	4.8 (0.8)	29.5 (6.7)	29.0 (7.0)	–18.8 (1.5)	–5.1 (0.4)	–4.5 (0.3)

TABLE 3. Average bimonthly dust flux from June 1994 through June 1996, and water-soluble composition of dust collected on the barren playa surface just west of the study area. Standard errors in parentheses.

Months	Dust flux (g m^{-2})	Sodium	Sulfate	Nitrate	Potassium	Boron
		g kg^{-1} dust		mg kg^{-1} dust		
Jul–Aug	81 (14.6)	171 (44)	27 (5.8)	704 (245)	2128 (462)	1302 (232)
Sep–Oct	17 (2.5)	120 (27)	33 (6.0)	884 (304)	1600 (429)	1547 (401)
Nov–Dec	172 (9.9)	193 (20)	94 (4.7)	565 (240)	2215 (140)	1712 (181)
Jan–Feb	159 (66.1)	150 (46)	45 (15.4)	6 (2.6)	2076 (629)	1592 (92)
Mar–Apr	157 (32.8)	151 (59)	41 (17.3)	293 (159)	1880 (159)	1414 (68)
May–Jun	239 (53.7)	136 (42)	21 (6.3)	23 (158)	1690 (355)	1316 (85)

coatings. Reduced conditions are likely facilitated by a shallow water table, but subdued oxygen diffusion rates through the fine-layered sediments may play a role. Lack of oxygen for root respiration will retard root growth of many plants (Marchner 1986). In addition, strongly reduced conditions will increase the solubility of metals such as Fe and Mn (Stumn and Morgan 1996). The unusually low pH in the 5th layer of vegetated soil 3 may be a consequence of changes in aeration status of the soil. If this horizon previously contained reduced sulfur minerals such as pyrite, its subsequent oxidation could lead to the low pH observed (Nordstrom 1982).

Natural History of Mounds

Vasek and Lund (1980) present a model of mound evolution on a playa that involves vegetation succession. Primary mound establishment on a playa begins with eolian dust entrapment by species of *Kochia*, which have high sodium tolerance. As mounds enlarge and accumulate nutrients, conditions are favorable for the establishment of *Atriplex lentiformis* ssp. *torreyi*, which promulgates mound expansion to a critical size at which time they coalesce. These complex mounds are favorable for the recruitment of new species such as *Atriplex confertifolia*, *Haplopappus acradenians*, and *Stanleya pinnata*. Further biogeochemical enrichment of the mound in Na^+, Cl^-, K^+, Ca^{+2}, and Mg^{+2} from litter fall and eolian dust leads to eventual death of plants and mound erosion. Soil pH and solute content are controlling factors in plant distribution in arid environments of the western United States (Gates et al. 1956, Skougard and Brotherson 1979).

There is no evidence to suggest plant succession occurs on mounds at Eagle Valley playa. Mounds begin and end with occupation by *A. occidentalis* and/or *S. vermiculatus*, and occasionally by *Atriplex confertifolia* and *Atriplex lentiformis* ssp. *torreyi*.

Mound establishment potentially could have begun sometime in the latest Pleistocene as pluvial Lake Lahontan dried (Mifflin and Wheat 1979, Morrison 1991). The mounds, however, are far younger because they lack profile differentiation indicative of nearly 10,000 yr of pedogenesis. For example, in a similar playa margin environment, a clay-rich, differentiated soil horizon formed in less than 3500 yr (Peterson 1980). Moreover, field research in the Lake

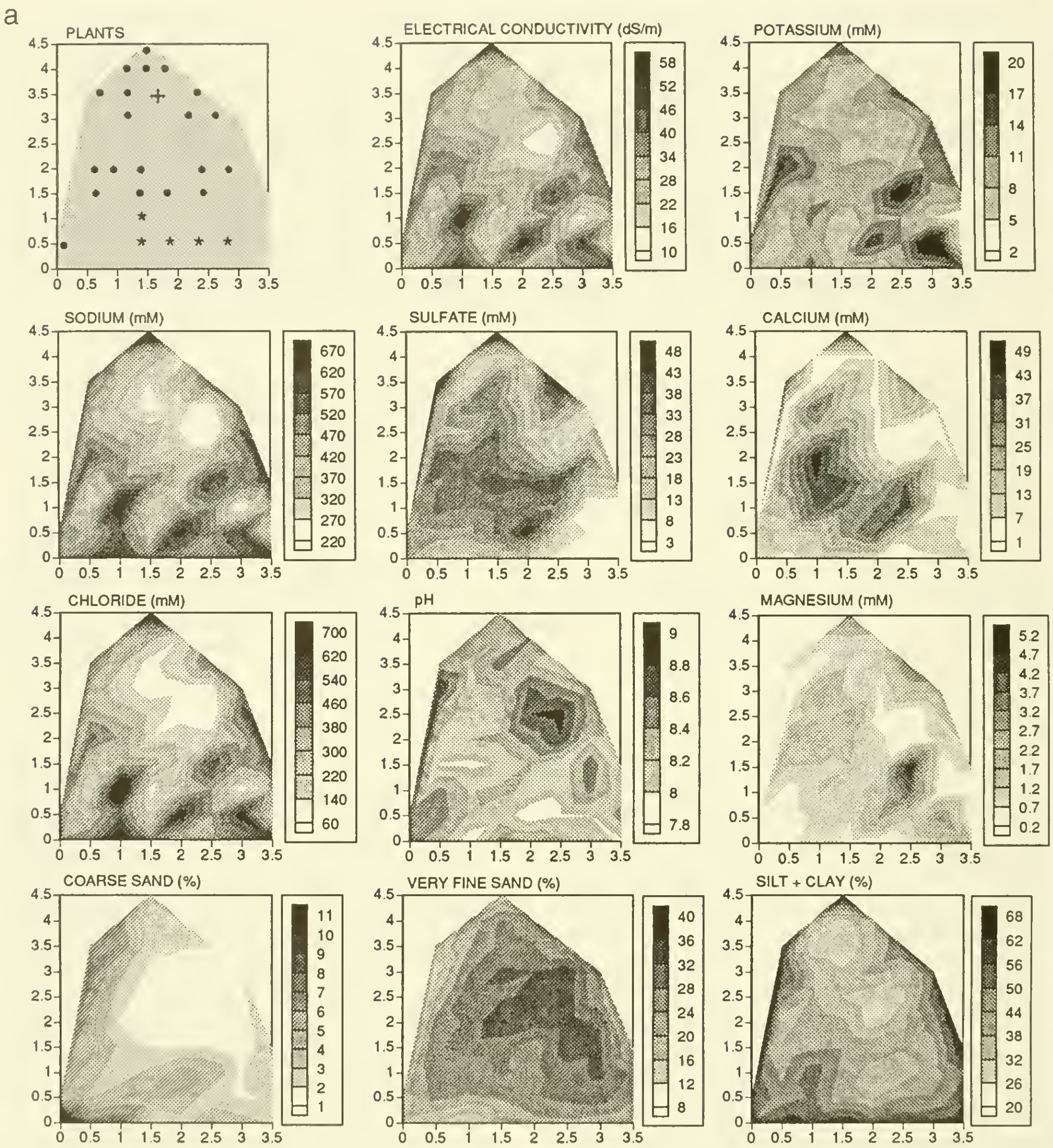

Fig. 3. Spatial distribution of aqueous extractable attributes for 3 mounds. If a portion of a plant canopy intercepted the grid sampling pattern, it is listed in the plants panel in the upper left-hand corner. Symbols used: ● = *A. occidentalis*, * = *S. vermiculatus*, and + = *A. torreyi*. Axes of graphs are in m. All panels are oriented north (top) to south (bottom).

Lahontan basin by Morrison (1964) shows that pedogenesis since the middle Holocene produces an oxidized B horizon.

The Holocene in the western United States has been marked by profound shifts in climate and vegetation patterns (Antevs 1938, Davis 1982, Wigand 1987, Anderson and Smith 1994). The latest Holocene has seen extended periods of drought lasting >100 yr (Stine 1994) and cooler and wetter periods where glaciers in the Sierra Nevada expanded considerably (Curry 1969). The late Holocene cool and wet periods or neoglacials contributed to the rise in pluvial lakes (Morrison 1964). Heights of neoglacial pluvial lake maximums are uncertain, but in all likelihood water at times completely covered the Eagle Valley embayment, further reducing the potential age of the mounds. Neal and Motts (1967) believe that most geomorphic features on and adjacent to playas in

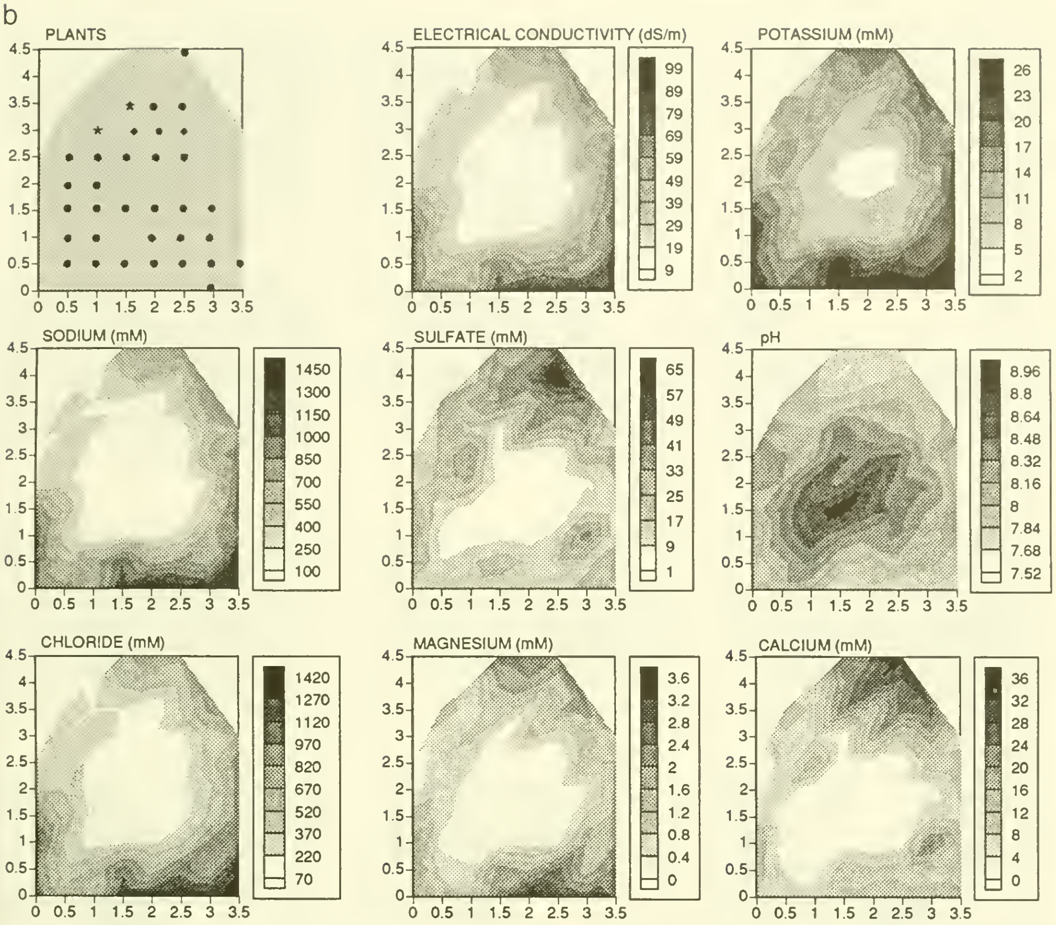
b
PLANTS
ELECTRICAL CONDUCTIVITY (dS/m)
99
89
79
69
59
49
39
29
19
9
POTASSIUM (mM)
26
23
20
17
14
11
8
5
2
SODIUM (mM)
1450
1300
1150
1000
850
700
550
400
250
100
SULFATE (mM)
65
57
49
41
33
25
17
9
1
pH
8.96
8.8
8.64
8.48
8.32
8.16
8
7.84
7.68
7.52
CHLORIDE (mM)
1420
1270
1120
970
820
670
520
370
220
70
MAGNESIUM (mM)
3.6
3.2
2.8
2.4
2
1.6
1.2
0.8
0.4
0
CALCIUM (mM)
36
32
28
24
20
16
12
8
4
0
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5

Fig. 3. Continued.

the western United States were formed within the last 100 yr, a result of a lowered water table caused by man's activities. The most recent glacial advance in the Sierra Nevada occurred from 1880 to 1908 (Curry 1969), which correlates with rings of *A. occidentalis* in the study area. Phytogenic hillocks can form and enlarge in this time frame (Gile 1966).

Present osmotic potentials of these playa margins are a magnitude too high for seed germination and suggest that large-scale plant recruitment may hinge on rare climatic events (Romo and Haferkamp 1987, Blank et al. 1994). What were those conditions in the past 90–120 yr that initiated mound formation? Present plant recruitment occurs rarely in small, flood-caused channels; however, mound plant demography suggests pulses of large-scale recruitment. If mound initiation began during a neoglacial cycle, then long-term increases in effective precipitation may have leached soluble salts deeper into the soil, thereby favoring plant recruitment. This scenario is problematic because long-term increases in effective precipitation would promulgate playa flooding. Perhaps plant recruitment on the playa margin began at the end of the neoglacial period. There would be greater sources of unconsolidated material at the delta of the Truckee River for mound building. Moreover, the neoglacial lake may have reduced the salt content of sediments along the playa margin.

Do mounds provide benefits for plants or are they happenstance, simply a result of inescapable physical processes? Phreatophytes such as *S. vermiculatus*, which dominantly root in the underlying lacustrine material, would seem not to require mound formation for continual survival. Potentially beneficial aspects of mound formation could include the following:

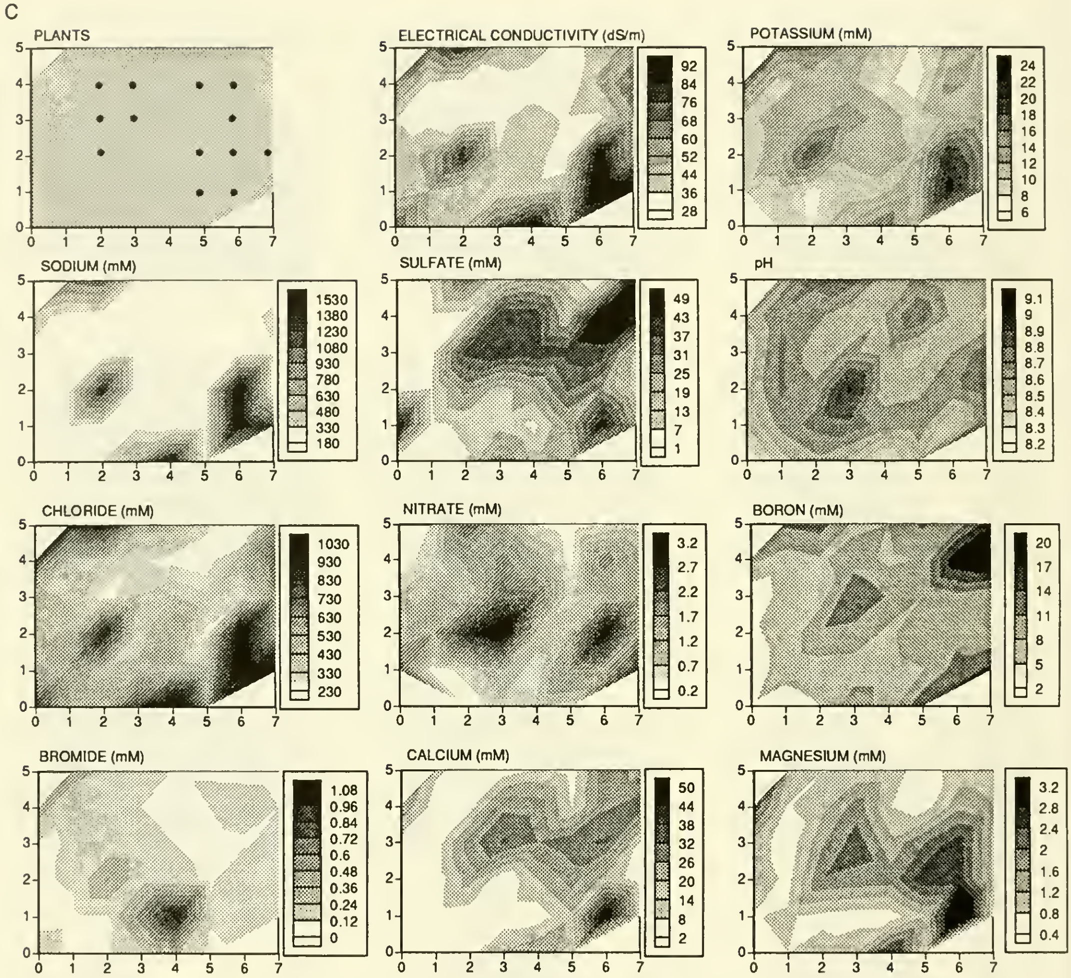
C
PLANTS
ELECTRICAL CONDUCTIVITY (dS/m)
92 84 76 68 60 52 44 36 28
POTASSIUM (mM)
24 22 20 18 16 14 12 10 8 6
SODIUM (mM)
1530 1380 1230 1080 930 780 630 480 330 180
SULFATE (mM)
49 43 37 31 25 19 13 7 1
pH
9.1 9 8.9 8.8 8.7 8.6 8.5 8.4 8.3 8.2
CHLORIDE (mM)
1030 930 830 730 630 530 430 330 230
NITRATE (mM)
3.2 2.7 2.2 1.7 1.2 0.7 0.2
BORON (mM)
20 17 14 11 8 5 2
BROMIDE (mM)
1.08 0.96 0.84 0.72 0.6 0.48 0.36 0.24 0.12 0
CALCIUM (mM)
50 44 38 32 26 20 14 8 2
MAGNESIUM (mM)
3.2 2.8 2.4 2 1.6 1.2 0.8 0.4
0 1 2 3 4 5 6 7
0 1 2 3 4 5

Fig. 3. Continued.

(1) a seedbed with superior physical characteristics and lower salt content favoring the recruitment of a host of plant species; (2) more favorable rooting media compared to the dense lacustrine sediments; (3) favorable bio-meteorological properties in portions of the mound due to aspect, i.e., cooler soil temperatures in midsummer on the north side of the mound or warmer temperatures in early spring on the south side of the mound.

At present, mounds function very poorly as seedbeds given the extraordinary levels of salt which would seem to negate beneficial aspect 1 listed above. Early in the life history of the mounds, however, they may have been far less saline. Throughout this study the salt content of recent eolian sand deposits on large dune fields and on the lee sides of mounds was measured. Electrical conductivity values of saturation extracts were always below 4 dS m^{-2}, indicating no osmotic limitation for germination of seeds of native plants. In the years of study, however, plant recruitment was never seen on the small eolian veneer on the sides of mounds, possibly because the veneers are too thin to allow a rooting mantle. It appears, then, that early in the life history of mounds, recruitment of plant species was not limited by salinity. Because of extreme periodicity of mound formation, we are witnessing mounds in Eagle Valley at an advanced age when extreme salinity prevents new plant recruitment. As established plants die, the no-longer-protected mounds will erode and new recruitment must await the next rare mound-building phase. Interestingly, soil description sites were revisited in

July 1997. All soil pits, which were not completely filled in with soil, have had extensive recruitment of plants. One pit has very robust plants of *A. lentiformis*, and *S. vermiculatus*.

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WINTER MACROINVERTEBRATE COMMUNITIES IN TWO MONTANE WYOMING STREAMS

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Frank A. Vertucci[3,5], and Sharon L. Dewey[6]

ABSTRACT.—Macroinvertebrate communities were examined on 4 winter dates over a 4-yr period in 2 high-altitude Rocky Mountain streams to document overwintering assemblages potentially experiencing spring acid pulses. Taxa richness values were comparable to other published lists for alpine and montane stream systems despite the fact that most literature reflected summer collections. Mean benthic density ranged from 1406 to 19,734 organisms/m², and drift rates ranged from 0 to 1740 organisms/100 m³. Benthic collections showed higher taxa richness than drift collections while the Ephemeroptera and Plecoptera occurred in greater proportions in drift than in benthos. The Nemouridae (Plecoptera), Ephemerellidae and Heptageniidae (Ephemeroptera), Chironomidae (Diptera), and Hydracarina were the numerically dominant taxa in benthic collections. Grazer/scrapers and shredder/detritivores were always the numerically dominant functional feeding groups at all sites, composing 60–90% of the benthos. Predators, constituting approximately 15% of the community, occurred in the same relative proportion at all sites on all dates. Winter macroinvertebrate communities in these low-order, montane streams exhibit high taxonomic richness and benthic densities as great as lower-elevation mountain streams in the West.

Key words: community structure, winter collections, stream insects, functional feeding groups, Wyoming, montane habitat.

Stream ecologists are interested in understanding the forces influencing community structure and composition. However, seasonal changes in habitat features might influence the relative importance of forces structuring stream communities (e.g., Peckarsky 1983, Minshall, Petersen, and Nimz 1985). Wiens (1977, 1981) argued that seasonal, multisite data were needed to make accurate assessments of community structure and resource use because of annual variation in population abundances within and among habitats. Harsh winter conditions (e.g., extreme cold, deep snowpack, ice cover) or the timing of insect life cycles often prevents stream ecologists from sampling some communities on a seasonal basis. Mountain streams, in particular, receive heavy snowfall, making most sites inaccessible during winter months. Yet, winter is the longest season of the year in mountain altitudes, retaining snow cover up to 7 mon.

Few studies have examined macroinvertebrate communities during mid- to late winter in mountain streams. Logan (1963), who sampled aquatic insects biweekly through the winter in Bridger Creek, Montana, found that Trichoptera larvae dominated the benthic taxa. Andrews and Minshall (1979) and Minshall (1981) sampled monthly throughout the year and found all common taxa during all seasons, but at different abundances. Communities sampled were dominated by grazer and collector functional feeding groups. Bruns and Minshall (1986) also sampled through the winter and showed an extreme change in winter niche parameters for the predator guild of an insect community in the Salmon River. They suggested that resource limitation (i.e., low prey numbers) in winter was a factor determining spatial resource partitioning in this system. However, these studies all focused on stream reaches at elevations below 3000 m. Studies at elevations exceeding 3000 m have been restricted primarily to the warmer, open-water season (Dodds and Hisaw 1925, Blake 1945, Elgmork and Saether 1965, Saether 1965, Allan

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1975, Short and Ward 1980, Ward and Berner 1980, Bushnell et al. 1982, 1986, Ward 1986).

Recent documentation of episodic acidification in mountain streams of the western U.S. (e.g., Williams and Melack 1991, Vertucci and Conrad 1994) suggests a need to understand winter stream communities if we are to assess potential impacts from snowmelt-related, spring pH declines. Winter samples collected immediately prior to any potential spring acid pulse could provide a reference picture of stream insect communities while reducing temporal difficulties associated with comparisons to later times of the year. Repeated, short-term acid events may have severe cumulative effects on stream communities in acid-sensitive streams of the West (Kratz et al. 1994). Impacts due to episodic pulses of acidity may reduce streamwater acid neutralizing capacity, influence fish community stability in small streams, and mobilize metals (Baker et al. 1996, Kiffney and Clements 1996, Wigington et al. 1996). Knowledge of winter community structure might enhance our ability to understand these episodic spring events. Our objective was to document the winter macroinvertebrate community structure in high mountain streams in Wyoming for a baseline reference in assessing snowmelt-driven, episodic acidification. We estimated winter benthic macroinvertebrate and drift density, taxonomic richness, and functional feeding group abundance for high-elevation streams having extensive snow cover.

METHODS

Study Area

Two streams were selected for study, West Glacier Lake Creek (WGL) and North Carbon Twin Lakes outlet (NCT). WGL is located within and NCT adjacent to the United States Forest Service Glacier Lakes Ecosystem Experiments Site (GLEES) (106°15′W longitude, 41°22′N latitude). GLEES was established to collect baseline and experimental data for assessing atmospheric deposition effects on sensitive alpine and subalpine ecosystems (Musselman 1994). An upstream and a downstream station were established on each stream such that the upstream station was located within a geologically acid-sensitive zone.

Stations WG and LB are located on WGL, T1 and T2 on NCT (Fig. 1). WG is at an elevation of 3250 m and approximately 150 m downstream from West Glacier Lake. LB, approximately 2 km downstream from WG at an elevation of 3163 m, is located approximately 100 m upstream from Little Brooklyn Lake. T1 is located at 3240 m elevation, approximately 75 m downstream of the easternmost North Carbon Twin Lake and within 100 m of treeline. T2 is approximately 0.25 km downstream from T1 at an elevation of 3230 m and 100 m downstream from the confluence of the eastern and western North Carbon Twin Lakes outflow (Fig. 1).

WG, LB, and T1 are 2nd-order streams, whereas T2 is a 3rd-order stream. Substrates at all sites consist of boulder, cobble and gravel. All sites are within forest habitat dominated by lodgepole pine (*Pinus contorta*) and Engelmann spruce (*Picea engelmannii*). Scattered stands of quaking aspen (*Populus tremuloides*) also occur near LB. All sites contain populations of brook trout (*Salvelinus fontinalis*). WG, LB, and T2 exhibit perennial flow while T1 experiences some zones of intermittent surface flow. The streams were sampled on 4 winter dates (November 1989, February 1990, 1991, and 1992).

Sampling Design

All sites except LB were snow covered on all sampling dates and required tunneling to reach the streams. We constructed 3 tunnels at each site on each date by digging through the snow to the stream banks and proceeding laterally until we reached the streams. Occasionally, tunnels opened directly over the stream. In such cases, we collected samples only upstream from the tunnel to reduce sampling bias associated with disturbance of the substrate. Snow depth (cm) was measured from the top of each tunnel to the ground.

On each date we took 3 Surber samples (1 sample per tunnel, 929 cm^2, 280-μm mesh) if water was present. All stones within the sampler were brushed to dislodge any organisms and the substrate was agitated to a depth of approximately 10 cm. Organisms were preserved in 80% EtOH in Whirl-Pac bags. In February 1991 and 1992, water was frozen or absent in some tunnels at T1 resulting in 2 and 1 Surber collections on those dates, respectively.

After completing benthic collections, we placed 1 drift net (l × h × w: 100 × 30 × 46 cm; 280-μm mesh) midstream in the upstream-most

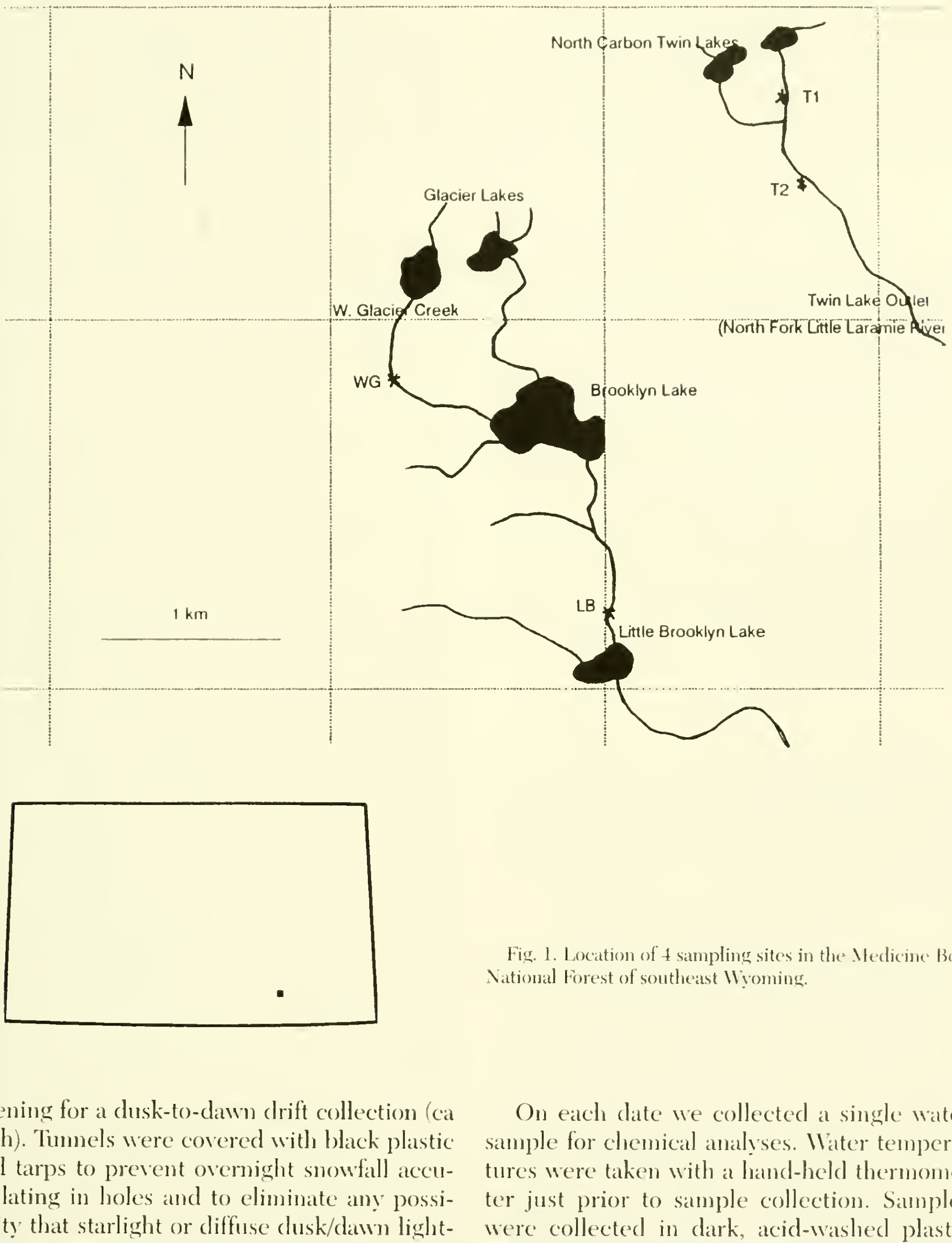

Fig. 1. Location of 4 sampling sites in the Medicine Bow National Forest of southeast Wyoming.

opening for a dusk-to-dawn drift collection (ca 12 h). Tunnels were covered with black plastic and tarps to prevent overnight snowfall accumulating in holes and to eliminate any possibility that starlight or diffuse dusk/dawn lighting might influence drift patterns. Stream volume filtered was estimated from the product of velocity, cross-sectional area, and duration of net set. Average velocity (Swoffer Model 2100 flow meter) and depth were based on 6 measurements, each from the mouth of nets upon placement and retrieval. Total set-time was recorded when nets were retrieved. Sample drift density (no./100m^3) was calculated according to Allan and Russek (1985).

On each date we collected a single water sample for chemical analyses. Water temperatures were taken with a hand-held thermometer just prior to sample collection. Samples were collected in dark, acid-washed plastic bottles, laboratory-filtered (Gelman 0.45-μm glass microfiber filters), and split into an acid-preserved (0.1 μl of 6.0 N nitric acid) and a nonpreserved subsample. Samples were refrigerated and usually analyzed within 48 h of collection. All samples were analyzed by the United States Forest Service Water Chemistry Laboratory in Fort Collins, CO. Major anions and cations were estimated on a Dionex 2010i ion chromatograph. Cations were also verified with a Smith-Hieftja 22 atomic absorption spectrophotometer. Conductivity was measured with a YSI conductance meter (Model 32). Acid neutralizing capacity (ANC) and pH were determined using an ARAS (Acid Rain Analysis System) radiometer.

Community Analysis

Macroinvertebrates were identified to the lowest possible taxonomic unit (usually species for insects except Diptera) using the following taxonomic keys: Allen and Edmunds 1962, Jensen 1966, Smith 1968, Edmunds et al. 1976, Baumann et al. 1977, Pennak 1978, Szczytko and Stewart 1979, Merritt and Cummins 1984, Klemm 1985, Peckarsky et al. 1985, Stewart and Stark 1988, and Ward and Kondratieff 1992; also G.T. Baxter, University of Wyoming, unpublished manuscript. Some taxa were verified by comparison to the Kansas Biological Survey (KBS) Reference Collection, to which new records were added. Functional feeding group designations followed tables in Merritt and Cummins (1984).

RESULTS

Data from November 1989 samples are omitted from any comparisons across years due to potentially confounding time effects. However, the November 1989 data are illustrated for completeness.

Physicochemical Analysis

Snow depths ranged from no cover (at LB in all years) to a maximum of 290 cm at WG in 1990 (Table 1). Generally, the 2 higher-elevation sites (WG and T1) had deeper snow cover than the 2 lower-elevation sites (LB and T2). Morning and evening water velocities were typically within 5 cm/sec of each other (Table 1). The minimum difference recorded was 0.3 cm/sec at T2 in 1992, the maximum 5.3 cm/sec at WG in 1990. Water depth rarely exceeded 10 cm. Surface ice was encountered only at T1 in 1991 and 1992, although all sites contained both anchor and frazil ice in varying amounts. Water temperature ranged from 0.3° to 1.8°C (Table 1).

All sites were characterized by circumneutral pH values (Table 2). WG had the lowest pH readings while LB always had the highest pH, ANC, and conductivity values. Mean conductivities ranged from 30.2 μS/cm at T1 to 138.0 μS/cm at LB. Major cation and anion concentrations varied across years and sites. Calcium and magnesium levels were 3–5 times greater at LB than at the remaining sites while anion levels were similar across sites and lowest at WG (Table 2).

Community Analyses

Of the 56 taxa we identified, no taxa occurred at all sites on all dates. Richness was greatest at LB in all years and lowest at T1 in all years (Appendix). Three sites (WG, LB, and T2) showed low year-to-year variation in richness values (CV = 10.4%, 9.8%, and 13.6%, respectively), whereas yearly variation in richness at T1 was higher (CV = 41.1%). Richness ranged from 9 (T1 in 1992) to 41 (LB in 1991).

All sites contained representatives of the 4 major functional groups. The grazer/scraper guild varied most annually (CV = 63.7%), whereas the predator guild varied least (CV = 25.1%). Grazer/scraper and shredder/detritivore groups dominated all sites; collectors were always least abundant (Fig. 2). Collectors represent the combined numbers of collector/gatherers and collector/filterers. Predators comprised approximately 15% of the communities at all sites on all dates.

Diptera composed the greatest proportion of the benthos (i.e., no. of Diptera in benthic samples/total no. in benthic samples) in all years at all sites except that in 1990 at T2 Ephemeroptera were highest (Fig. 3). On average, Nemouridae (Plecoptera), Baetidae (Ephemeroptera), and Hydracarina were the other numerical dominants in the benthos (Appendix). Few taxa were found at all sites on all dates. The most ubiquitous taxa included Plecoptera (*Sweltza lamba*, *Zapada haysi*, and *Z. cinctipes*), Ephemeroptera (*Ephemerella infrequens*, *Cinygmula* sp., and *Baetis bicaudatus*), and Trichoptera (*Rhyacophila brunnea* and *R. verrula*; Appendix). Seven taxa (*Plumiperla diversa*, *Paraleuctra vershina*, *Arctopsyche grandis*, *Rhyacophila pellisa*, *Anagapetus* sp., *Lepidostoma* sp., and *Oligophlebodes minutus*) were collected only from LB. Trichoptera always accounted for <10% of the benthic community.

Diptera and Ephemeroptera comprised the greatest proportion of drifting taxa (e.g., no. of Diptera drifting/total no. drifting), whereas Trichoptera and Hydracarina constituted the least (Fig. 4). Proportions of Ephemeroptera

TABLE 1. Mean winter stream conditions (± $s_{\bar{x}}$; $n = 3$) at 4 sampling sites on 4 sampling dates. For ice cover, N = none present; Y = present. For water depth, $n = 6$. Temperature is a single a.m. reading.

	Year/Site															
	November 1989				February 1990				February 1991				February 1992			
Parameter	WG	LB	T1	T2	WG	LB	T1	T2	WG	LB	T1	T2	WG	LB	T1	T2
Snow depth (cm)	122.0	0	125.0	61.0	290.0	0	180.0	110.0	225.0	0	150.0	94.0	250.0	0	170.0	100.0
	(7.0)		(8.7)	(13.1)	(20.8)		(17.3)	(5.0)	(11.2)		(13.9)	(9.8)	(12.1)		(14.8)	(14.4)
Velocity (cm/s)																
p.m.	20.0	9.3	9.8	9.3	13.6	4.6	7.3	7.0	4.0	20.0	<1.0	7.0	6.1	<1.0	n/a	1.3
	(3.2)	(1.1)	(2.0)	(1.5)	(1.4)	(0.2)	(0.6)	(0.8)	(0.6)	(1.7)		(0.4)	(0.2)			(0.1)
a.m.	20.0	9.0	8.9	8.3	8.3	2.0	n/a	n/a	8.0	18.1	<1.0	12.0	7.3	<1.0	n/a	1.0
	(1.1)	(1.1)	(1.5)	(1.7)	(1.1)	(0.1)			(0.3)	(0.9)		(1.2)	(0.2)			(0.1)
Water depth (cm)	9.9	5.5	8.4	7.6	7.4	11.4	6.0	5.4	12.7	3.7	11.0	9.4	4.7	3.3	n/a	5.3
	(0.3)	(0.6)	(0.7)	(0.1)	(0.6)	(1.4)	(0.5)	(1.5)	(0.1)	(0.6)	(0.2)	(1.1)	(0.1)	(0.4)		(1.1)
Temperature (°C)	0.5	2.0	1.0	0.8	0.5	1.8	0.3	n/a	0.3	1.0	1.0	1.0	0.4	1.0	n/a	1.0
Ice cover	N	N	N	N	N	N	N	N	N	N	Y	N	N	N	Y	N

TABLE 2. Mean stream water chemistry for 3 February sampling dates (±$s_{\bar{x}}$). All measurements are µEq/l except conductivity and pH. Conductivity is µS/cm. ANC = acid neutralizing capacity.

	Site			
	WG	LB	T1	T2
pH	6.9 (0.12)	8.0 (0.06)	7.0 (0.06)	6.9 (0.14)
Conductivity	30.0 (14.32)	138.0 (12.99)	30.2 (1.20)	31.4 (1.49)
ANC	255.1 (85.35)	1473.6 (83.66)	199.7 (11.35)	238.4 (9.06)
Calcium	177.6 (51.07)	938.5 (126.66)	139.2 (6.71)	156.2 (6.58)
Magnesium	100.8 (24.99)	523.5 (25.34)	65.6 (0.28)	79.9 (2.49)
Sodium	13.6 (0.99)	22.6 (1.41)	42.2 (1.68)	29.9 (1.54)
Potassium	6.2 (0.75)	16.4 (0.47)	8.8 (1.06)	7.5 (0.35)
Ammonium	1.3 (0.95)	2.2 (1.69)	1.8 (0.48)	0.9 (0.78)
Chloride	3.9 (0.97)	3.6 (1.83)	7.6 (1.03)	4.8 (0.56)
Sulfate	22.3 (1.35)	27.6 (0.90)	22.9 (2.68)	22.2 (0.92)
Nitrate	7.8 (1.55)	12.9 (2.46)	25.7 (10.35)	10.6 (1.24)

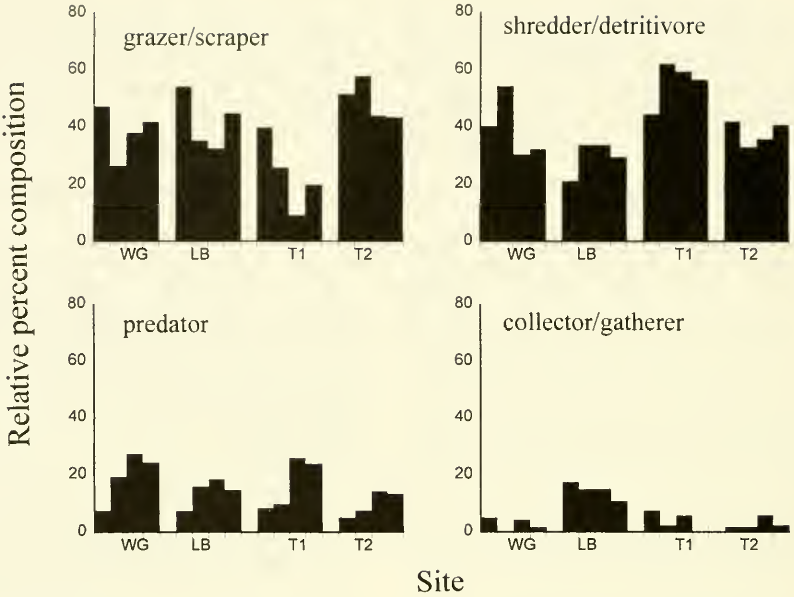

Fig. 2. Relative percent composition of functional feeding groups in the benthos during winter months in 2 mountain streams. From left to right, bars reflect samples collected in November 1989, February 1990, 1991, and 1992, respectively.

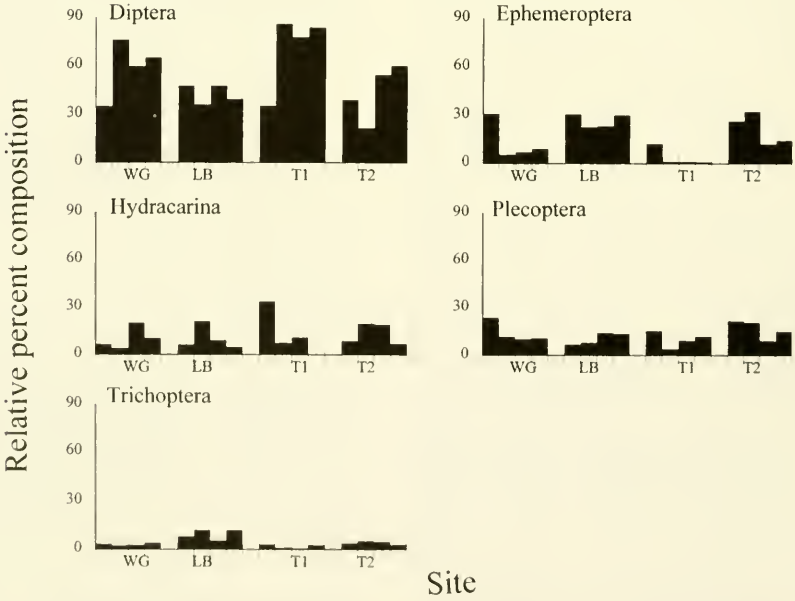

Fig. 3. Relative percent composition of major orders in the benthos. From left to right, bars reflect samples collected in November 1989, February 1990, 1991, and 1992, respectively.

and Plecoptera in drift samples exceeded benthic proportions while Diptera occurred in lower proportions in the drift relative to benthos. Hydracarina and Trichoptera were approximately equally represented in benthos and drift (Figs. 3, 4).

The mean number of organisms in the benthos (no./m^2) ranged from <1500 to >15,000 organisms (Fig. 5). Chironomidae were always the most numerous. Sample drift densities generally ranged from 100 to 600 organisms per 100 m^3 and showed no consistent pattern across sites or times (Fig. 6).

DISCUSSION

Unlike other faunistic studies in mountain stream habitats, this study examined macroinvertebrate communities in 2 high-elevation streams under winter conditions. Taxonomic richness observed in this study was slightly higher than summer faunal surveys from other western mountain streams (Ward 1975, 1986). As expected, the highest richness values were found at the lower-elevation sites LB and T2. Also, the 3 sites with permanent water flow exhibited lower annual variation in richness values (CVs < 15%) than T1, which had no flow on 1 of 4 dates. Community composition was similar to that recorded by Kondratieff (1994) during a qualitative summer collection of aquatic macroinvertebrates from lakes and streams in the GLEES area. He collected 72 taxa during that study. While this represents 16 taxa more than we collected during this study, his collections focused on littoral zones of lakes and streams and were made during summer months. Our samples were all collected during winter from streams only and within midstream microhabitats.

Functional feeding groups in these streams during winter were compositionally similar to, yet proportionally different from, summer collections in other mountain streams and fit well with expectations of an expanded river continuum concept (RCC; Vannote et al. 1980, Minshall et al. 1985). We found the grazer/scraper guild present in higher proportions and collector/gatherers in lower proportions than might be expected for low-order, eastern woodland streams, which are expected to be heavily shaded by riparian canopies that limit autochthonous food resources (Vannote et al. 1980). However, new syntheses of the RCC incorporate the effects of local lithology/geomorphology on insect community development. These high-elevation streams are near the treeline in relatively open woodlands where potential autochthonous production is expected to be high, offering ample food resources for the grazer/scraper guild. These patterns suggest that the RCC predicts well for the grazer/scraper guild in high-elevation western streams. Further study is warranted on these streams to correlate grazer/scraper abundance with algal productivity under winter conditions.

Shredders were the other dominant functional guild, composed primarily of nemourid stoneflies. This contrasts with results of Short and Ward (1980) for a stream of similar altitude (though a summer study) in which shredders constituted a much smaller percentage of the benthos, but were still primarily nemourid stoneflies. Their study site flowed through a meadow while our sites were principally within forested reaches, potentially offering higher quantities of allochthonous material for shredders. Also, our functional guild is a mix of shredders and detritivores. Possibly, the detritus feeders dominate these sites and the shredders are of less importance.

Proportions of the major insect orders were similar to many other mountain stream studies (e.g., Saether 1965, Allan 1975, Ward 1975, 1986, Short and Ward 1980, Minshall 1981), even though most studies reflect summer collections. Diptera (primarily Chironomidae) and Ephemeroptera were always the most numerous taxa in our study. In general, Ephemeroptera and Plecoptera occurred in greater proportions in the drift than in the benthos while the reverse was observed for the remaining orders, indicating that mayflies and stoneflies are more prone to drift than the remaining taxa. However, drifting mayflies and stoneflies were predominantly early instar Baetidae and Nemouridae, suggesting that these 2 groups are winter active or more susceptible to passive drift than the remaining taxa.

Hydracarina often exceeded Plecoptera and Trichoptera in benthic abundance, an occurrence not generally reported. Because other faunal surveys, based primarily on summer collections and focusing on insects, have not included the Hydracarina, comparisons are difficult to make. However, failure to include the Hydracarina in community analyses will overemphasize proportions of remaining

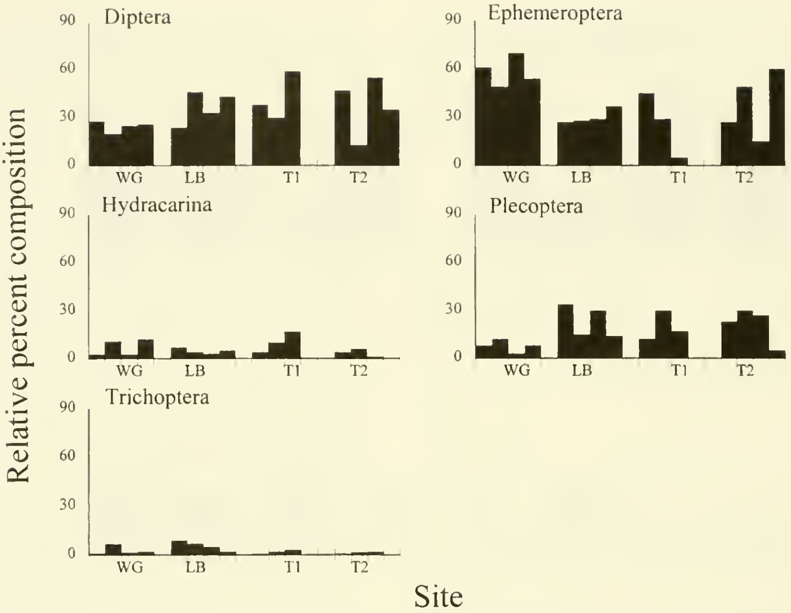

Fig. 4. Relative percent composition of major orders in the drift. From left to right, bars reflect samples collected in November 1989, February 1990, 1991, and 1992, respectively.

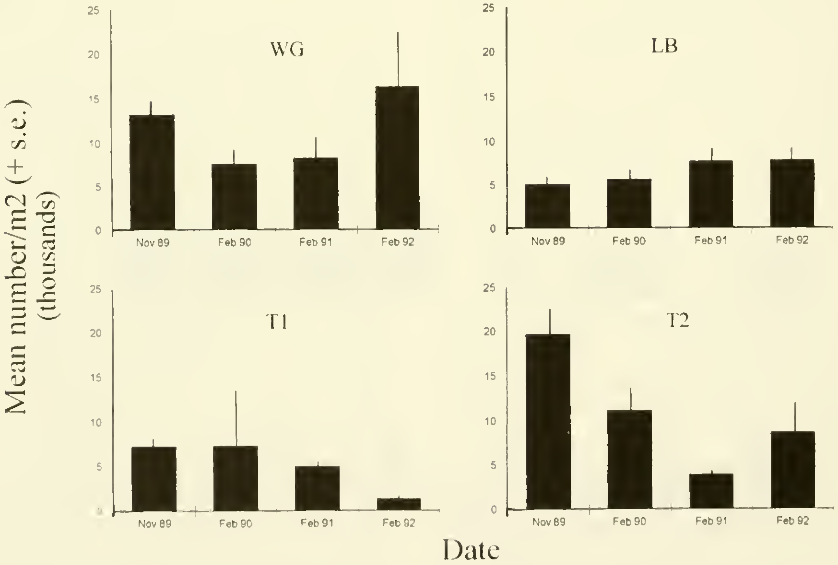

Fig. 5. Mean ($n = 3$) density of benthic organisms (no./m^2). Only 2 and 1 samples were collected for T1 in 1991 and 1992, respectively. Error bars are $+s_{\bar{x}}$.

community members. Most Hydracarina are predatory as adults or parasitic as larvae (Pennak 1978) and may have significant impacts on macroinvertebrate numbers. Drift estimates changed little with or without inclusion of the Hydracarina.

Total density of benthic organisms in these streams was very high compared to other mountain streams of similar altitude (Short and Ward 1980) but comparable to estimates made by Minshall (1981) in a lower-altitude stream reach. However, mesh sizes in all our nets

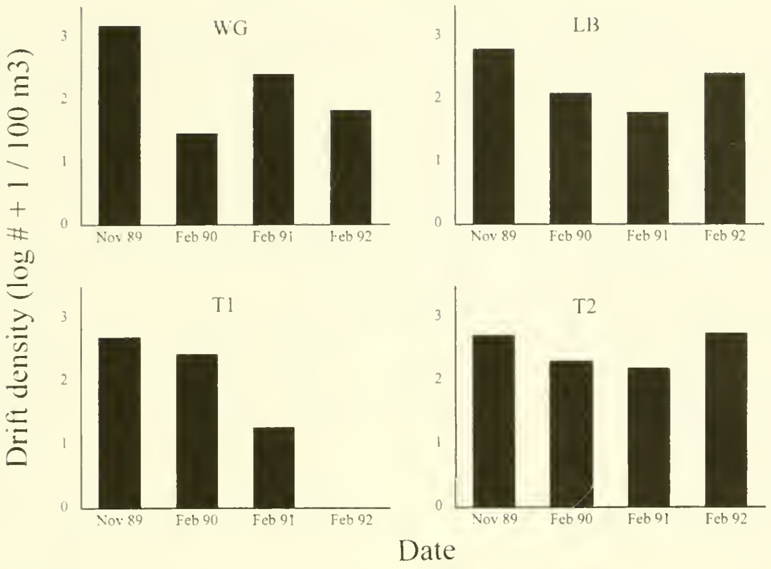

Fig. 6. Sample drift density (no./100m^3) for all organisms.

were considerably smaller than those used by Short and Ward (280 µm in our study vs. 700 µm in theirs); thus, the range of sizes captured was greater. Maximum densities exceeded 15,000 organisms/m^2 on some dates, but were usually nearer 5000/m^2. We expected low organism abundance during our winter sampling because egg diapause was a suspected life history attribute of some community members, especially within the Trichoptera and Ephemeroptera (e.g., see tables in Merritt and Cummins 1984). The great abundance of small (≤ 2 mm) Baetidae (Ephemeroptera) during November sampling suggests they have a short incubation period prior to hatching. Minshall (1981) also reported the Baetidae occurred in high abundance during winter months in an Idaho stream.

Density of drifting organisms was not particularly high relative to summer drift collections in other high-elevation streams (Allan 1987). Because we did not record diel periodicity in drift, it is hard to ascertain whether this proximal cue is important during winter. In fact, under prolonged darkness it is possible that drift is equally abundant at all hours of day and night. Extended periods of darkness may reduce insect susceptibility to predation by visual-feeding fishes, resulting in high drift densities. Likewise, drift rates might be high if encounters with predatory invertebrates increase (Peckarsky 1980, Soluk and Collins 1988) because the predators are also released from fish predation constraints.

This study provides a preliminary assessment of winter macroinvertebrate community structure in high-elevation streams and suggests that winter communities are diverse and numerically abundant. Though Vertucci and Conrad (1994) documented spring acid pulses in some glacial-melt headwater streams of GLEES, winter pH in our sites was circumneutral, indicating that pH depressions do not begin until early snowmelt. Similarly, the macroinvertebrate community composition was not indicative of one stressed by acidity. Further studies comparing these communities in different seasons may provide insights to the role of seasonal heterogeneity in community ecology.

Although winter stream conditions are harsh (i.e., extreme cold, reduced flow, lack of sunlight), there may be less variability in key abiotic parameters during this season than at other times of the year. For example, stream flow and temperature are 2 critical features for aquatic insect ecology and biology (Hynes 1970, Ward 1989). Variation in stream discharge and velocity during winter is minimal because cloudbursts and thaws, which may lead to rapid discharge increases, do not occur. Temperature fluctuations are also minimized because there are no direct effects from solar radiation as streams are snow covered. These observations suggest that winter may be a time when physical habitat features exhibit low temporal heterogeneity (sensu Kolasa and Rollo 1991) and may influence winter community structure. Likewise, the recent documentation of episodic acidification associated with spring snowmelt in the West (Vertucci and Conrad 1994) suggests a need for greater understanding of winter community structure. A knowledge of overwintering communities will help us accurately assess the effects of these episodic events. Also, seasonal comparisons of community structure and function and a detailed focus on winter stream dynamics may further our understanding of the forces important in structuring stream communities.

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The appendix follows on the next 3 pages.

APPENDIX. Benthic abundance at 4 sampling locations on 4 sampling dates. The 4 numbers under each site are the total number of each taxa collected in 3 pooled Surber samples in November 1989, and February 1990, 1991, and 1992, respectively. Only 2 and 1 samples were taken from T1 in 1991 and 1992, respectively. Functional group categories are based on Merritt and Cummins (1984): P = predator, C/G = collector/gatherer, S/D = shredder/detritivore, G/S = grazer/scraper.

Taxa	Site																Functional group
	WG				LB				T1				T2				
Plecoptera																	
PERLODIDAE																	
Isoperla quinquepunctata	1	2	11	8	4	2	5	5	4	0	3	0	0	9	1	4	P
I. fulva	4	0	4	8	6	3	0	5	9	8	1	3	2	12	0	6	P
I. petersoni	1	1	0	0	0	0	0	3	0	1	0	0	0	0	0	1	P
Cultus sp.	0	0	0	0	0	16	5	0	0	0	0	0	0	0	0	11	P
Kogotus modestus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	P
Megarcys signata	2	0	2	4	1	0	1	0	0	0	0	0	0	0	0	0	P
Unidentified perlodid	14	4	0	0	7	0	2	0	2	0	0	1	19	0	0	3	
CHLOROPERLIDAE																	
Sweltza lamba	32	23	72	98	22	12	107	112	23	0	24	9	1	43	0	31	P
Suwallia spp.	5	0	9	25	0	0	13	20	0	0	1	0	1	2	1	0	P
Plumiperla diversa	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	S/D
Triznaka signata	0	0	2	0	0	0	0	0	0	0	8	0	19	0	0	0	S/D
Unidentified chloroperlid	174	18	0	0	219	41	0	0	8	2	0	0	10	3	0	0	
LEUCTRIDAE																	
Paraleutra vershina	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	S/D
NEMOURIDAE																	
Zapada haysi	758	210	90	270	16	46	48	73	181	80	50	26	764	240	35	116	S/D
Z. cinctipes	79	10	49	77	43	32	89	59	86	0	41	0	349	338	63	194	S/D
Malenka coloradensis	0	0	0	0	5	6	5	0	0	0	1	0	57	6	0	0	S/D
Prostia besametsa	0	0	0	0	0	2	0	0	10	0	0	0	0	0	0	0	S/D
CAPNIIDAE																	
Capnia spp.	0	0	0	0	0	4	30	23	0	1	0	0	0	0	0	2	S/D
Ephemeroptera																	
EPHEMERELLIDAE																	
Drunella coloradensis	0	0	0	0	20	58	101	164	0	0	0	0	5	11	0	0	S/D
D. doddsi	30	5	1	6	10	6	7	3	2	0	0	0	20	7	4	6	S/D
Ephemerella infrequens	100	0	13	5	58	53	52	32	30	0	7	0	40	9	12	5	S/D
Serratella sp.	0	0	0	0	17	0	3	0	5	0	0	0	0	0	0	0	S/D
LEPTOPHLEBIIDAE																	
Paraleptophlebia debilis	0	0	0	0	37	22	65	86	1	0	0	0	0	0	0	2	C/G
SIPHLONURIDAE																	
Ameletus velox	8	0	5	10	0	0	6	0	11	3	2	0	8	5	5	7	C/G

Appendix. Continued.

Taxa	Site																Functional group
	WC				LB				T1				T2				
Heptageniidae																	
Rhithrogena spp.	0	0	0	2	0	17	4	12	0	0	0	0	0	15	1	3	C/G
Cinygmula spp.	199	67	88	253	110	76	88	293	83	4	5	3	108	457	37	130	G/S
Baetidae																	
Baetis bicaudatus	810	43	58	139	83	80	69	37	119	20	2	0	1276	495	71	177	G/S
B. tricaudatus	0	0	0	0	100	44	102	31	0	0	0	0	0	11	5	18	G/S
Trichoptera																	
Hydropsychidae																	
Arctopsyche grandis	0	0	0	0	1	2	0	2	0	0	0	0	0	0	0	0	C/G
Rhyacophilidae																	
Rhyacophila pellisa	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0	P
R. brunnea	51	45	21	67	11	42	10	22	13	6	3	1	76	54	26	44	P
R. verrula	40	10	6	56	2	28	27	14	4	4	0	1	37	15	10	8	P
R. coloradensis	25	0	0	0	3	0	0	0	0	0	0	0	10	1	3	1	P
Glossosomatidae																	
Glossosoma spp.	5	0	0	6	6	11	9	14	0	0	0	0	10	1	3	1	G/S
Anagapetus spp.	0	0	0	0	6	6	1	0	0	0	0	0	0	0	0	0	G/S
Uenoidae																	
Neothremma sp.	0	0	0	6	0	2	3	9	0	0	0	0	0	0	0	0	G/S
Brachycentridae																	
Micrasema sp.	0	1	2	0	40	56	26	33	0	0	0	0	0	0	0	0	S/D
Lepidostomatidae																	
Lepidostoma sp.	0	0	0	0	6	17	4	4	0	0	0	0	0	0	0	0	S/D
Hydroptilidae																	
Agraylea sp.	5	0	31	52	0	2	0	0	47	10	7	6	85	94	12	13	G/S
Limnephilidae																	
Ecclisomyia maculosa	0	0	2	0	1	7	9	1	0	0	0	0	0	1	0	2	C/G
Dicosmoecus atripes	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	S/D
Oligophlebodes minutus	0	0	0	0	35	21	28	160	0	0	0	0	0	0	0	0	G/S
Diptera																	
Chironomidae	1300	1617	1380	3960	680	70	1020	870	720	764	1086	146	2154	681	600	1460	
Tipulidae	11	37	22	2	23	0	1	17	4	10	21	0	18	9	12	8	
Ceratopogonidae	6	4	0	24	22	5	5	0	0	0	0	0	31	0	0	0	
Dixidae	2	4	0	0	4	3	5	0	2	0	0	0	2	0	2	0	

APPENDIX. Continued.

Taxa	Site																Functional group
	WG				LB				T1				T2				
Coleoptera																	
DYTICIDAE																	
Hygrotus spp.	0	0	1	2	1	0	0	0	1	0	0	0	1	3	9	2	P
ELMIDAE																	
Cleptelmis sp.	0	0	0	0	0	0	2	1	0	0	0	0	2	0	0	2	C/G
Heterlimnius corpulentis	0	0	0	0	9	14	15	17	1	0	0	0	9	13	12	47	C/G
Narpus sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	C/G
Miscellaneous																	
Oligochaeta																	
Limnodrilus sp.	0	1	0	0	8	6	5	5	16	2	4	0	11	29	0	22	
Mollusca																	
Pelecypoda																	
Sphaerium sp.	17	14	4	26	0	5	2	0	7	0	10	0	11	3	23	15	
Collembola	0	0	2	0	0	0	0	0	0	1	0	0	6	1	4	0	
Ostracoda	27	15	38	580	0	16	161	65	0	0	0	0	3	0	0	6	
Hydracarina	240	89	466	485	91	333	196	109	685	152	170	21	488	618	695	172	
Turbellaria	8	3	40	106	1	7	2	48	0	0	0	0	0	0	0	0	
TAXA RICHNESS	28	22	26	26	41	37	41	33	26	17	19	9	31	32	24	32	

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RANGE OF THE BROWN-HEADED COWBIRD IN COLORADO: PAST AND PRESENT

Jameson F. Chace[1] and Alexander Cruz[1]

ABSTRACT.—The historic range of the bison (*Bison bison*) on the Great Plains has been well documented. In Colorado the range of bison included both the eastern grasslands and higher-elevation ridges and mountain parks, up to an elevation of 3900 m. Based on the commensal relationship of the brood-parasitic Brown-headed Cowbird (*Molothrus ater*) with the bison, we suggest that the cowbird had a larger historical elevational range in Colorado than previously known and consequently has had a long-term host-parasite relationship with high-elevation breeding songbirds.

Key words: Brown-headed Cowbird, Molothrus ater, *bison,* Bison bison, *range expansion, Colorado.*

The Brown-headed Cowbird (*Molothrus ater*) is a well-studied obligate brood parasite (Rothstein 1975, Friedmann et al. 1977, Rothstein 1990, Robinson et al. 1995, Cook et al. in press) that historically occupied a range similar to that of the bison (*Bison bison;* Friedmann 1929). Cowbirds ranged over the Great Plains in commensal association with bison; these "buffalo birds" are thought to have foraged among the grazed grasslands for insects stirred up by herd movements (Friedmann 1929, Mayfield 1965). They later expanded their range with the clearing of forests and introduction of domestic livestock (Mayfield 1965, Rothstein 1994). In Colorado, Brown-headed Cowbirds have undergone a recent elevational range expansion, possibly due to habitat alteration and cattle grazing in the high country (Hanka 1985), similar to cowbirds in the Sierra Nevada Range (Rothstein et al. 1980, Rothstein 1994).

The historical range of bison on the Great Plains is well documented (Allen 1877, Roe 1970). In addition, bison in the Rocky Mountains historically ranged above timberline in Montana, Wyoming, and Colorado (Fryxell 1926, 1928, Warren 1927, Beidleman 1955, Pattie and Verbeek 1967). Bison once ranged throughout most of Colorado west of the Great Plains and at all elevations (Armstrong 1972, Meaney and Van Vuren 1993). Furthermore, bison probably were relatively abundant throughout northwestern Colorado, South Park, Middle Park, North Park, and the Front Range (Armstrong 1972, Meaney and Van Vuren 1993). We suggest that because of their commensal relationship cowbirds also occurred at high elevations in Colorado until their range contracted with the extirpation of bison and that they have undergone an elevational range re-expansion with the introduction of domestic livestock.

Our purpose is to demonstrate that (1) the 1st observations of cowbirds in Colorado occurred during the time lapse between extirpation of bison from, and movement of cattle into, higher elevations, and (2) the number of high-elevation records of cowbirds increased as the number of cattle in the western counties increased. Implications of long-term host-parasite interactions in Colorado's high-elevation region are discussed.

METHODS

We reviewed records of cowbird parasitism (see Chace and Cruz 1996) and bison distribution and determined the timing and abundance of cattle introductions to the Colorado counties west of the Great Plains. We also reviewed Colorado agriculture statistics to obtain the number of cattle in each county per year from 1883 to 1985 (intermittent years missing). Colorado counties east and west of the Front Range were analyzed separately, with Front Range counties containing >40% grassland habitat designated as eastern (see Fig. 1 for delineation of counties). Cattle numbers were summed per year by eastern and western designation. Although

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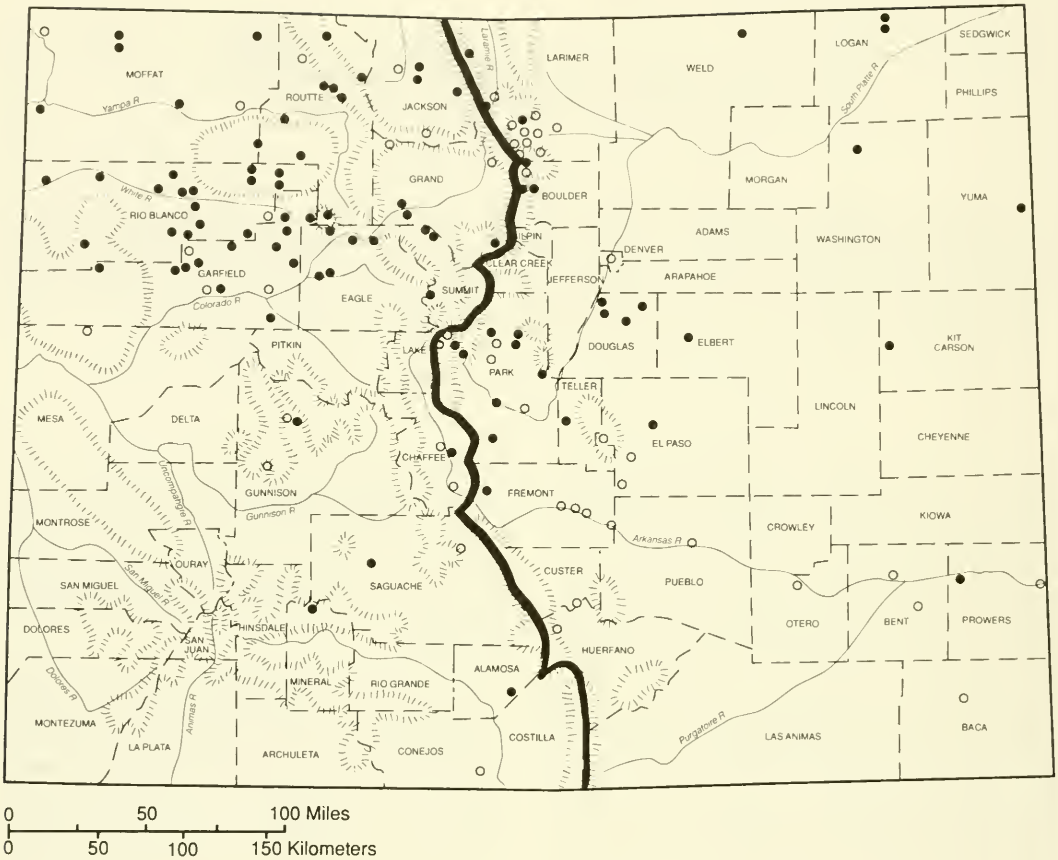
MOFFAT
ROUTTE
JACKSON
LARIMER
Laramie R
WELD
LOGAN
SEDGWICK
PHILLIPS
South Platte R
Yampa R
RIO BLANCO
White R
GRAND
BOULDER
MORGAN
YUMA
GARFIELD
EAGLE
SUMMIT
GILPIN
CLEAR CREEK
JEFFERSON
DENVER
ADAMS
ARAPAHOE
WASHINGTON
Colorado R
PITKIN
LAKE
PARK
DOUGLAS
ELBERT
KIT CARSON
TELLER
LINCOLN
MESA
DELTA
GUNNISON
CHAFFEE
EL PASO
CHEYENNE
Uncompahgre R
MONTROSE
Gunnison R
FREMONT
CROWLEY
KIOWA
Arkansas R
OURAY
SAN MIGUEL
San Miguel R
SAGUACHE
CUSTER
PUEBLO
OTERO
BENT
PROWERS
DOLORES
HINSDALE
SAN JUAN
HUERFANO
Dolores R
MINERAL
RIO GRANDE
ALAMOSA
MONTEZUMA
Animas R
LA PLATA
ARCHULETA
CONEJOS
COSTILLA
Purgatoire R
LAS ANIMAS
BACA
0 50 100 Miles
0 50 100 150 Kilometers

Fig.1. Recent distribution of bison (*Bison bison*) in Colorado with emphasis on the region west of the Great Plains. Solid circles represent specimen localities. Open circles represent localities extracted from literature. Central line delineates Colorado counties west of the Great Plains. Map and information taken from Meaney and Van Vuren (1993) with permission of the Denver Museum of Natural History.

cattle are not the only livestock that attract cowbirds (Rothstein et al. 1980), they are by far the most numerous and probably are a good index of livestock numbers per county in general.

RESULTS

Meaney and Van Vuren (1993) recorded all known bison specimens in Colorado west of the Great Plains from which we calculated that of 116 bison specimens, 56.9% were collected above 2500 m (Table 1). Recent research on free-ranging bison has shown that bison have seasonal elevational movements through open ponderosa pine (*Pinus ponderosa*), pinon-juniper woodlands (*P. monophylla* and *Juniperus scopulorum*), and across subalpine forest–parkland habitat (Fuller 1962, Van Vuren 1983, Van Vuren and Bray 1986, Shaw and Carter 1990). Furthermore, based on specimens taken (Figgins 1933), some herds of bison wintered in the mountain parks and migrated into higher elevations through forested communities during the summer (Meaney and Van Vuren 1993). Extant free-ranging bison in forested montane habitat of the Henry Mountains of Utah have smaller group sizes (2–30 animals) and larger home ranges (52 km^2) than bison of the Great Plains (Van Vuren 1983, Van Vuren and Bray 1986, Meaney and Van Vuren 1993). In Colorado, Benedict (1993 personal communication) speculates that bison were extirpated from the Estes Park area by 1859 primarily due to the effects of the harsh winter of 1843–44. That winter, in combination with market hunting, may have been the cause of bison decline in other parts of the state. The last known wild

TABLE 1. Elevational distribution of bison specimens in 22 Colorado counties west of the Great Plains (from Meaney and Van Vuren 1993).

Elevation (m)	No. of specimens (N = 116)
3501+	13
3001–3500	21
2501–3000	32
2001–2500	36
1500–2000	14

bison in Colorado were killed in 1897 in Park County (Cory 1912), although a few may have survived until 1904 (Warren 1906).

Bison numbers were very low by 1883 when cattle were fairly abundant east of the Continental Divide in Colorado (268,585 head), with considerably fewer in the western counties (56,782 head; Colorado Department of Agriculture, Colorado Agriculture Statistics, 1883–1985). Nearly equal numbers of cattle occurred in eastern and western counties through the 1920s (Fig. 2). Western counties reached their present levels of cattle population by 1959, with a peak in 1974 (829,300 head; Fig. 2). From 1941 the number of cattle in eastern counties consistently was double the number west of the plains, with a peak in 1973 of 2,978,800 head (Fig. 2).

Records of cowbird parasitism or presence rarely mention exact elevational localities. Early naturalists in Colorado surveyed high elevations and found cowbirds primarily occurring in grasslands and foothills below 2500 m (Henshaw 1875, Drew 1885, Gale 1893, Cooke 1897, Sclater 1912). More recently, cowbirds have been noted at higher elevations. Keeler-Wolf et al. (1972) reported parasitism of a Yellow Warbler (*Dendroica petechia*) nest in Gunnison County (2895 m). Cowbirds were common in mountain parks and river valleys in 1977 and 1978, with observations up to 2890 m in Park, Lake, Jackson, and Larimer counties (Hanka 1985). From 1986 to 1989, 164 Brown-headed Cowbirds were trapped and banded at a feeding station on Mt. Evans (elevation 3260 m). Cowbirds were trapped from April to August, with highest numbers in May (mean = 29.0); males outnumbered females 2.35:1 (Lorraine E. Reiner unpublished data). Hanka (1985) reported parasitism of Brewer's Blackbirds (*Euphagus cyanocephalus*) at 2895 m in north central Colorado. Spencer (1985) reported an adult Wilson's Warbler (*Wilsonia pusilla*) feeding a young cowbird at 3180 m. Wilson's Warblers were also reported to be parasitized in Boulder, Clear Creek, and Summit counties (Elisabeth Ammon unpublished data). In 1993–94 cowbirds parasitized Warbling Vireo (*Vireo gilvus*) nests ca 3000 m in Boulder County (Chace unpublished data). Recently, a number of high-elevation records of parasitism have been reported in the Colorado Breeding Bird Atlas project (Table 2; Colorado Breeding Bird Atlas unpublished data).

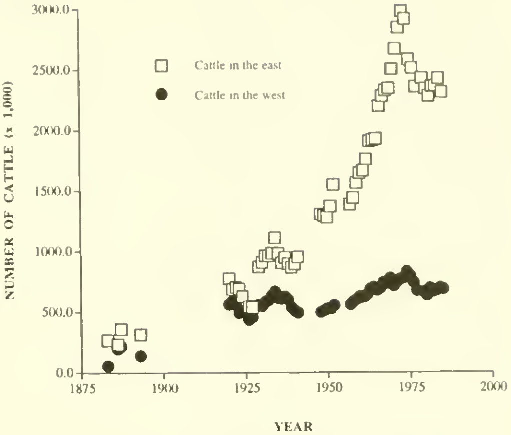

Fig. 2. Number of cattle in eastern and western Colorado (1883–1985).

DISCUSSION

In Colorado, cowbirds probably had a historical, geographical, temporal, and elevational distribution similar to that of the bison, with an upper elevational limit ca 3800 m. Bison probably were numerous enough in the mountains to support commensal flocks of cowbirds during the avian breeding season. As the bison approached extirpation in the mid-1800s, herds were small and scattered, and cowbirds would have been mostly restricted to lower elevations where cattle were just beginning to show appreciable numbers in Colorado (Fig. 1). Cowbirds likely became associated with cattle in eastern Colorado and began to re-expand their range following the growing cattle herds to the west. By the turn of the century, naturalists began to record avian distributions in Colorado. Even though higher elevations were surveyed (Drew 1885, Sclater 1912), cowbirds were found primarily from grasslands to foothills and mountain

TABLE 2. Records of cowbird parasitism from western high-elevation counties from the Colorado Breeding Bird Atlas (1987–1994).

Species	Years	Counties
Willow Flycatcher (*Empidonax trailii*)	1987	Jackson
Dusky Flycatcher (*Empidonax oberholseri*)	1994, 1995	Jackson, Eagle
Cordilleran Flycatcher (*Empidonax difficilis*)	1991	Teller
Hermit Thrush (*Catharus guttatus*)	1990, 1994	Park, Mineral
Warbling Vireo (*Vireo gilvus*)	1988, 1993, 1994	Gunnison, Fremont, Montrose
Virginia's Warbler (*Vermivora virginiae*)	1994	Teller
Yellow Warbler (*Dendroica petechia*)	1987, 1993, 1994	Grand, Gunnison, Jackson
Yellow-rumped Warbler (*Dendroica coronata*)	1991	Routt
MacGillvray's Warbler (*Oporornis tolmiei*)	1994	Gunnison
Wilson's Warbler (*Wilsonia pusilla*)	1988	Summit
Green-tailed Towhee (*Pipilo chlorurus*)	1991, 1993	Routt, Montrose
Fox Sparrow (*Passerella iliaca*)	1993, 1994	Eagle, Grand, Summit
Song Sparrow (*Melospiza melodia*)	1995	Teller
Lincoln Sparrow (*Melospiza lincolnii*)	1994	Park
Gray-headed Junco (*Junco hyemalis*)	1991, 1993	Grand, Gunnison
Brewer's Blackbird (*Euphagus cyanocephalus*)	1991	Gunnison

parks, <2500 m (Henshaw 1875, Gale 1893, Cooke 1897), although Friedmann (1929) reported an observation of a female cowbird in association with horses at 2895 m in Colorado. It was not until 1958 that the total number of cattle in Colorado rose above 2 million head. After 1958 cattle numbers remained high and stable in western counties, while the number of cattle would double in eastern counties by 1973. Shortly after this time, cowbirds were found breeding at high elevations, ca 2800 m (Keeler-Wolf et al. 1972, Hanka 1985). These data suggest that Brown-headed Cowbirds occurred at high elevations in Colorado until the extirpation of bison and have recently regained their former range with introduction of domestic livestock.

In Colorado the center of bison abundance was the eastern grasslands. Although bison have been recorded in high montane areas in central and northwestern Colorado, records are conspicuously absent from the southwestern corner of the state (Meaney and Van Vuren 1993). Cowbirds are known from the eastern portion of the state, but little is known about their distribution in the west prior to the bison extirpation. They probably were located along the major tributaries to the Colorado River (Rothstein 1994) and were associated with western bison herds. Following cattle introductions, western populations of cowbirds may also have re-expanded their elevational distribution; however, a distributional change has not been well documented. In all probability the elevational range re-expansion was bimodal, but more pronounced along the eastern edge of the Rocky Mountains.

Prior to the extirpation of bison in the mid-1800s, Brown-headed Cowbirds undoubtedly bred and parasitized the nests of many songbird species in high-elevation regions of Colorado. It is likely that cowbird numbers at higher elevations declined as bison were extirpated and resurged following the introduction of cattle. However, now a different pattern of cowbird parasitism probably exists. When cowbirds followed nomadic bison herds, their parasitic efforts and eggs were dispersed over the range of seasonal movements of bison herds, whereas now cowbird breeding populations are as stationary as the herds of livestock around which they forage. Implications of this changing pattern on songbird communities are likely very important. Where once songbird communities may have encountered brood parasitism for only a portion of their breeding season, now the pressure of parasitism is pronounced throughout their reproductive effort. In addition, because of the strong site fidelity of many songbirds (Greenwood and Harvey 1982, Holmes and Sherry 1992), parasitism pressure may exist throughout the lifetime reproductive effort of many individual birds.

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CHEMICAL AND BIOLOGICAL CHARACTERISTICS OF DESERT ROCK POOLS IN INTERMITTENT STREAMS OF CAPITOL REEF NATIONAL PARK, UTAH

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ABSTRACT.—Chemical variability and biological communities of rock pools found in small desert drainage basins of Capitol Reef National Park were characterized over 8 mon in 1994. Neither flooding, drying, nor the presence or absence of surrounding vegetated wetlands had a great effect on chemical composition, which was very dilute and fluctuated somewhat in response to rain events. Neither flooding nor drying affected the composition of biological communities in the pools. Summer storms affected only a few drainages at a time, and only a few study pools of significant volume dried completely during the hot, dry summer. This suggests that only a portion of the Waterpocket Fold aquatic community is ever disturbed at a time, leaving undisturbed areas as a source of recovery. Pools bordered by vegetated wetlands always supported greater numbers of species throughout the year than those bordered only by bedrock, but the same taxa were found in both vegetated and bedrock pools. The rock pool fauna in Capitol Reef National Park appear to be resilient to climatic variability.

Key words: desert rock pools, aquatic invertebrates, aquatic chemistry, disturbance, Capitol Reef National Park, Utah.

Aquatic environments in the arid Colorado Plateau are extremely important resources for the maintenance of desert ecosystems. Many aquatic resources are ephemeral, characterized by spatial and temporal discontinuities in flow (Grimm and Fisher 1992). Ephemeral streams may flow after storms and snowmelt, but surface water rapidly becomes confined to pools as the running water evaporates or is transpired (Poff and Ward 1989).

The Waterpocket Fold is a 62 × 1.25-km (100 × 2-mi) ridge of exposed Navajo sandstone that runs the length of Capitol Reef National Park, Utah (Fig. 1). The Waterpocket Fold contains many small drainages cut laterally across its width due to water erosion. These small drainages represent an extreme example of ephemeral streams. Cut directly into sandstone bedrock, these drainages function as streams only a few days each year. Stream flow occurs during and immediately after rain or snowmelt. Between precipitation events, water resides in rock pools, many of which are large enough that they rarely dry out. Pools are of 2 morphologies: those cut directly into sandstone with no surrounding vegetation, and those with riparian vegetation borders. Sandy alluvial deposits that support vegetation also allow groundwater storage. Vegetation surrounding these pools grades from obligate wetland species such as *Typha latifolia* (cattail), *Salix* spp. (willows), *Phragmites australis* (reed), and *Carex* spp. (sedges) to upland species common in surrounding desert shrub, pinyon-juniper, and slickrock communities (Spence and Henderson 1993). Spence and Henderson (1993) found an increase in the number and abundance of nonnative species associated with pools where cattle grazing had previously occurred, suggesting that these systems are vulnerable to such disturbance.

Limited information has been collected on desert rock pools along the Waterpocket Fold in Capitol Reef National Park. Previous investigations have addressed questions regarding the role of disturbance by flooding on aquatic organisms (Haefner and Lindahl 1988, 1991). Similar systems of the Colorado Plateau have received more attention, including a chemical characterization of rock pools in northern Arizona (Van Haverbeke 1990), biological characterizations of temporary pools near Moab, Utah (Dodson 1987), and ecosystem-scale studies in Sycamore Creek, Arizona (Gray and Fisher 1981, Fisher et al. 1982, Grimm and Fisher 1992). We conducted a 6-mon intensive study to assess the status of physical and biological resources as the essential 1st step in managing

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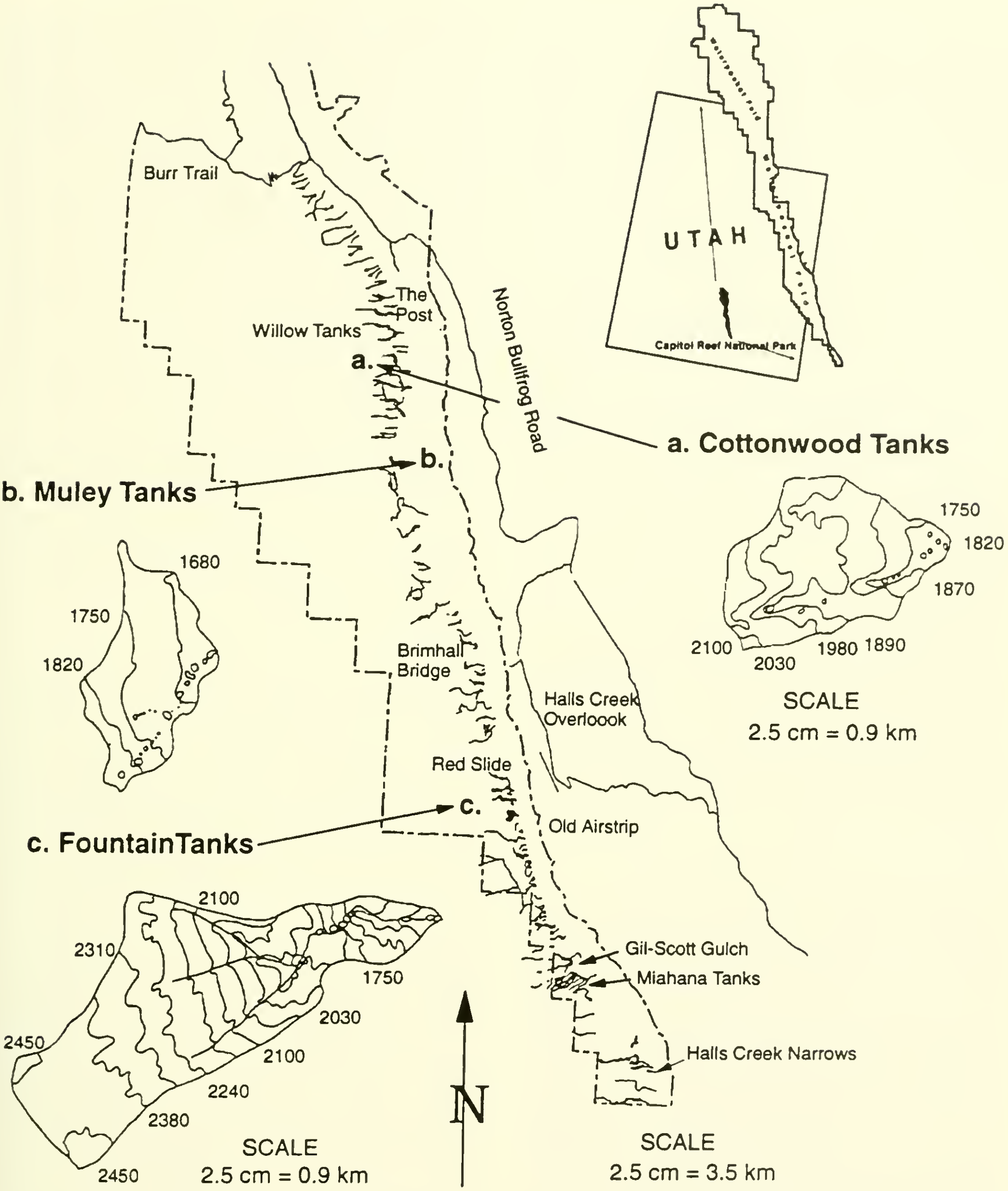
UTAH
Capitol Reef National Park
Burr Trail
The Post
Willow Tanks
a.
Norton Bullfrog Road
a. Cottonwood Tanks
b.
b. Muley Tanks
1750
1820
1870
2100
2030
1980
1890
SCALE
2.5 cm = 0.9 km
1680
1750
1820
Brimhall Bridge
Halls Creek Overloook
Red Slide
c.
c. FountainTanks
Old Airstrip
2100
2310
1750
2030
2450
2100
2240
2380
2450
SCALE
2.5 cm = 0.9 km
Gil-Scott Gulch
Miahana Tanks
Halls Creek Narrows
N
SCALE
2.5 cm = 3.5 km

Fig. 1. Map showing location of Capitol Reef National Park and enlargements of the 3 study drainages where both chemical and biological analyses were conducted: (a) Cottonwood Tanks, (b) Muley Tanks, and (c) Fountain Tanks. Contour lines on enlargements are in meters.

natural resources (Stohlgren et al. 1995). This study complemented a larger survey of 460 rock pools in 80 major drainages (Berghoff 1994). We explored temporal and spatial variability of pools to answer several questions: How variable is pool chemistry and ecology over time and space? Does the presence of surrounding vegetation influence water quality, pool volume, or ecology? How important are flooding and drought as disturbances to both water quality and aquatic invertebrate community composition?

SITE DESCRIPTION

The Waterpocket Fold, also known as Capitol Reef, is a north–south trending monocline of Navajo Sandstone that extends approximately 112 km north from Lake Powell in southern Utah (Fig. 1). The Waterpocket Fold is specifically named for the more than 460 waterpockets, or rock pools, that have been carved by water and scouring action in the many small west–east drainages cut into the sandstone. Drainages are typically <2 km long and are made up of a series of pools connected with a drainage depression that conducts water during and after precipitation events. Because there is no upwelling of groundwater in the Navajo Sandstone (Kimball 1988), precipitation is the only source of new water to these drainages. Rock pools range in volume from a few liters to >1000 m^3. Some vegetated wetlands adjacent to pools can have sediment depths up to 2 m.

Mean annual precipitation ranges from 183 mm at Fruita (Capitol Reef NP headquarters) in the north to 140 mm near Lake Powell. The maximum mean July temperature is 33°C, while the minimum mean January temperature is –8°C (Spence and Henderson 1993, National Oceanic and Atmospheric Administration 1994).

METHODS

Studies were centered on 5 drainages in the southern part of Capitol Reef National Park: Cottonwood, Muley, Fountain, and Miahana Tanks, and Gil-Scott Gulch (Fig. 1). Each drainage supported pools with and without surrounding vegetation, from which we selected 2 pools with and 2 pools without vegetation for in-depth study. Those with surrounding vegetation were classified as either palustrine emergent or palustrine scrub-shrub wetlands (Cowardin et al. 1992). Bedrock-bordered pools were classified as lacustrine littoral (Cowardin et al. 1992). Drainages ranged from broad and open at Muley Tanks to long and narrow at Cottonwood. The headwaters of Cottonwood Tanks originate in a narrow slot canyon. We made an attempt to select drainages along a broad length of the Waterpocket Fold. To test the results of flooding, we chose pools from among larger, more permanent water bodies so that they would have water in them when July and August storms were expected. In spite of this selection objective, some pools dried out.

Precipitation and Pool Volume

We placed rain gages near the top and bottom of each drainage and monitored them weekly. Each gage was a funnel that drained to a coiled tygon tube connected to a plastic liter bottle. There were slight differences in the amounts collected by each pair of gages, but since we were unable to determine whether differences were due to precipitation variability or to gage catch efficiency, we used the gage that reported the greatest total precipitation for the summer to represent rain for each drainage. Past experience has suggested it is very difficult to overcollect precipitation in harsh environments, so the maximum amount recorded is more likely to represent actual rainfall than is a statistical average of 2 gages (Baron 1992). The volume of intensively studied rock pools was measured weekly by geometrical approximation using an algebraic formula for a half ellipse, and the depth of water was measured with a meter tape.

Chemical Analyses

Samples were collected approximately every other week from 1 pool with surrounding vegetation and 1 pool without surrounding vegetated wetlands in Cottonwood, Muley, and Fountain Tanks between March and August 1994. We collected 23 samples from Cottonwood Tanks (13 from vegetated and 10 from unvegetated pools), 22 from Muley Tanks (11 from each pool type), and 21 from Fountain Tanks (11 from vegetated and 10 from unvegetated pools). Water samples were collected in 125-mL high-density polyethylene (HDPE) bottles that had been acid-washed in 10% HCl solution, rinsed, and stored full of deionized water prior to sampling for pH and specific conductance. Samples collected for major ion analyses were stored in 250-mL HDPE bottles that had also been acid-washed with the same procedures. Because samples could not be refrigerated immediately, major ion samples were preserved with 0.5 mL chloroform (Keene et al. 1986). Samples were filtered in the field with a Nalgene hand pump through Whatman GF/C filters into baked dark-colored borosilicate glass bottles for analysis of dissolved organic carbon. Water temperature was recorded at the time of sampling.

Specific conductivity and pH of water samples were determined weekly using a conductivity (Amber Science Inc. Model 604) and pH meter (Beckman Model 21). For summary statistics pH was converted to H^+ concentrations, averaged, and then reconverted to pH. Because pH values can vary diurnally according to algal photosynthetic activity and we did not standardize sample collection times to account for this, pH values should be viewed as approximate, rather than absolute. Preserved samples were analyzed for major ions within 3–4 mon after sample collection. Aliquots were filtered (Whatman GF/C filters) for cation analyses. Major ions were analyzed with ion chromatography, and alkalinity was analyzed with a Gran titration at the USFS Rocky Mountain Forest and Range Experiment Station in Fort Collins, Colorado (O'Deen et al. 1994). Dissolved organic carbon (DOC) was analyzed by the USGS Water Resources Division in Boulder, Colorado (Oceanography International Model 700 carbon analyzer). Quality of the chemical analyses was assessed by calculating the ion percent difference (IPD) between positively and negatively charged ions. This is an important component of being able to interpret results with confidence. All but 2 of the samples met 15% cutoff criteria for acceptable IPD at ionic strengths of greater than 200 µeq/L; these 2 data samples were discarded (Stensland and Bowersox 1984, O'Deen et al. 1994). Eight DOC samples were collected in duplicate; they compared within 10% over a range of 3–32 mg C/L.

Comparisons of mean chemical characteristics between the 3 drainages were made using a Student-Newman-Keuls test for studentized range. The studentized range is the difference between the largest and smallest treatment means divided by an estimate of the standard error of each single treatment mean. Separation of the means in the rank order influences the size of the difference required for significance (Ferguson 1981).

Comparison of the chemistry of pools adjacent to vegetated wetlands with pools surrounded by sandstone was done with a Wilcoxon matched pairs signed-rank test. Because the test assumes independence between the 2 groups being compared, we used a reduced data set. Connection of the pools during flooding events invalidates the assumption of independence. No vegetated versus unvegetated comparisons were run for Cottonwood drainage, since rain events caused observed flow between the Cottonwood pools through July and August. Pools in Muley drainage were separated all summer, as no rain event was strong enough to cause spillage from the top pools. Pools in Fountain drainage overflowed only once, in late July. Chemical analyses after the flooding event in Fountain were excluded from the analysis.

Biological Analyses

We sampled aquatic fauna from macrozooplankton to vertebrates weekly from 4 pools in each drainage March through August 1994. Additional collections were made in September 1993 and January, February, and September 1994. Macrofauna were defined as any animals larger than the mesh size (1 mm^2) of a standard dip-net. Based upon previous laboratory identifications, we field identified organisms to the lowest practical taxon, usually species, and noted their life history stage (juvenile or adult). Bottle-trap and light-trap collections were used for specific identification of adult insects. A voucher collection of the invertebrate samples has been deposited in the C.P. Gillette Museum of Arthropod Diversity at Colorado State University.

Semi-quantitative measures of abundance were recorded as a rank based upon 3 standard dip-net sweeps of each pool. The sweeps were taken from different sides of the pool and the samples were combined in a single white pan. Organisms were placed into taxa and ranked 0 (no individuals), 1 (1–10 individuals), 2 (11–50 individuals), or 3 (51+ individuals). Three additional sweeps were then taken to insure consistent monitoring of rare species, and any taxa found that were not present in the first 3 sweeps were given an abundance rank of 1. Organisms were returned to the pool after enumeration and identification.

Common methods for quantitatively sampling the pools were field tested in February and March 1994. These were found to be unreliable and destructive. In such small systems it was important to sample nondestructively to avoid affecting pool communities through direct removal of pool organisms. Both a 30-micron plankton tow and standard Ekman dredge produced variance as large as population means. The rock pool organisms do not, however, fit other characteristics expected of a Poisson distribution that would exhibit this variance (Bhattacharyya and Johnson 1977). Rock pool communities cannot be assumed to be independent of each other, but are affected by the previous community. Standard sampling methods also were subject to other problems, such as not accounting for patchiness of pool organisms and escape tactics by most adult beetles and hemipterans. The portable box method (Dodson 1987) of quantification, which was found suitable only for shallow pools of <1.2 m, was ineffective for quantifying the more abundant benthos such as chironomid larvae.

Cluster analysis and a transformed Pearson correlation matrix using 22 species were used to examine the biological structure of rock pool communities. Species chosen included all species present on a given sampling day and represent the major functional groups as well as the most abundant pool fauna. Pearson correlation coefficients among each species' abundance for a given period were transformed into a distance measure, and the data were then treated as distances in a cluster analysis to determine whether or not groups of organisms could be considered nonrandomly associated. Groups of species that appeared together as clusters between zero and 0.3 were considered nonrandom associations. This analysis was performed 3 times, using data from the weeks of 15 March, 10 June, and 14 July.

The effect of disturbance, defined as flooding, on the number of species present and ratio of juvenile to adult life history stages was evaluated with *t* tests. The effect of pool volume and temperature on biological parameters was examined with Pearson correlation coefficients.

RESULTS

Hydrology

The summer of 1994 was unusually dry, even for Capitol Reef National Park. Total precipitation at Cottonwood, Muley, and Fountain Tanks was 66.1, 27.2, and 31.0 mm, respectively (Fig. 2). According to the 38-yr record analyzed by Spence and Henderson (1993), 1/3 of the annual precipitation, 46–60 mm, usually falls as thunderstorms in July and August (Julian dates 182–243). In 1994 the July and August combined precipitation was 22.7, 5.0, and 31.9 mm at Cottonwood, Muley, and Fountain Tanks, respectively.

Volumes of the 6 intensively studied pools with vegetation increased with rain events, although only 5 events over the entire sampling period caused flooding, defined as overflow from the pools. Maximum measured volumes ranged from 325 to 800 m^3 for pools bordered by vegetation and 50 to 635 m^3 for pools bordered by bedrock. Minimum volumes of 0–150 m^3 were measured for pools bordered by vegetation and 5–150 m^3 for pools bordered by bedrock. Major flash floods did not occur during the study period, although flooding was observed in Cottonwood and Fountain Tanks, but not in Muley Tanks. Normalized pool volume values (against maximum measured volume) with time showed that pool volumes covaried with rain events for pools with and without surrounding vegetation (Fig. 2). There appeared to be less variation in volume of pools with surrounding vegetation and soils, presumably because of the effects of evapotranspiration and soil water storage.

Pool water temperatures warmed over the summer from March to mid-April lows (4–18°C) to highs (32–35°C) in June, July, and August (Fig. 3). After mid-April most pool waters had temperatures in the 22–25°C range, regardless of location, exposure, or whether they were bordered by vegetated wetlands or bedrock. Pools were sampled at different times of day. Temperatures indicated in Figure 3 should be interpreted as within a range of measured temperatures for any given week because of wide diurnal variability.

Chemical Characterization

The waters of the rock pools we sampled were dilute, with specific conductivities <200 μS/cm and pH values near 7.0. The ionic ratio of calcium to alkalinity in the pools was similar to that measured from groundwater wells of the Navajo Sandstone (calcium:alkalinity of 0.4 in the pools compared with 0.3 reported from well samples by Kimball 1988), although the pools were far more dilute. Ratios of calcium:silica (>20) and calcium:sulfate (>8) did not compare well to those in groundwater (calcium:silica <5, calcium:sulfate <2). While silica can be consumed by diatoms, it is more likely that mineralogical variation in the bedrock and far less water residence time in the pools account for the different chemistries between groundwater and surface water.

Phosphate, an essential and often limiting nutrient, was never measured in concentrations above detection limits. Nitrate concentrations

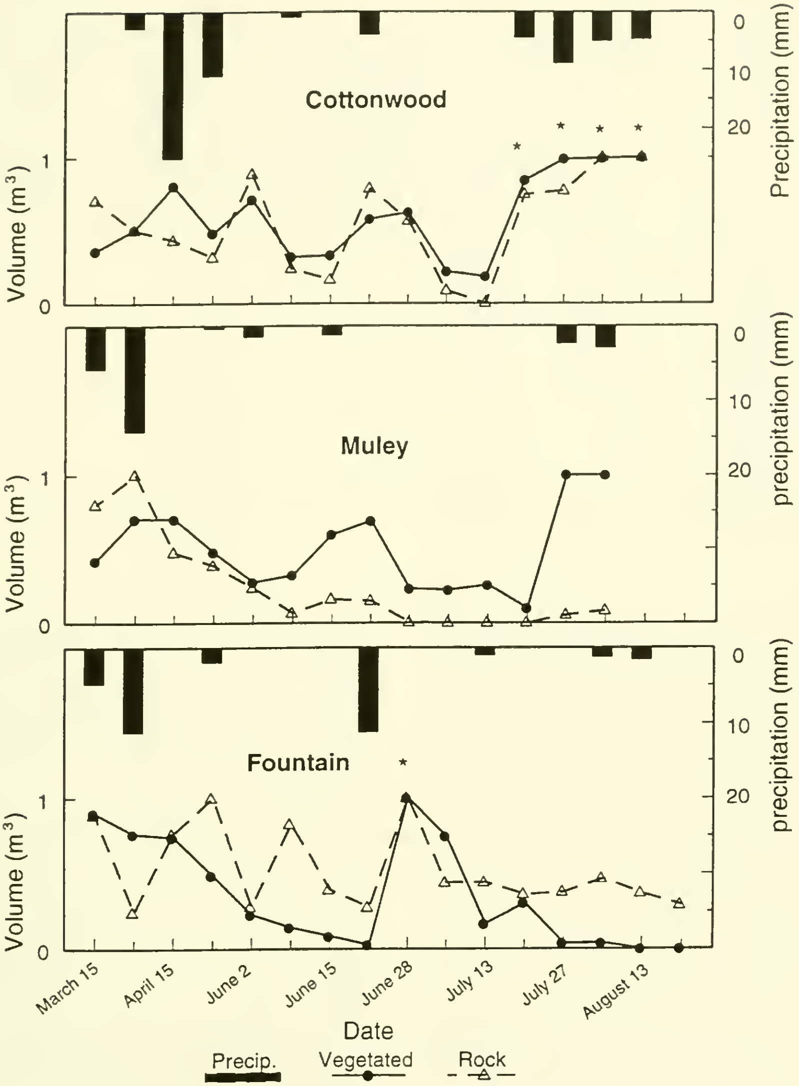

Fig. 2. Precipitation (bars) and normalized (against maximum measured volume) pool volumes (lines) for Cottonwood, Muley, and Fountain Tanks drainages during the period of study, March–August 1994. Rain events that caused flooding are marked with an asterisk. Flooding was defined as overflow from one pool to another.

were also low, while ammonium was present in somewhat higher concentrations.

Alkalinity and conductivity were similar in concentration to those reported by Fisher and Grimm (1983) for an ephemeral desert stream, and conductivity was similar to that reported by Van Haverbeke (1990) for ephemeral rock pools. Nitrate was somewhat lower in concentration in the study pools than reported for the ephemeral stream in Arizona (Fisher and Grimm 1983). Nitrate concentrations of 4.8–6.5 μmol/L were much lower than those measured in summer wet precipitation from the 2 nearest National Atmospheric Deposition Program sites, Green River and Bryce Canyon, Utah. Summer volume-weighted mean nitrate concentrations at these 2 sites were 29.1 μmol/L and 43.4 μmol/L, respectively (NADP/NTN 1996).

Sulfate concentrations in Cottonwood and Muley Tanks (21.9 μmol/L and 27.1 μmol/L, respectively) were similar to sulfate measured in precipitation (10.7 μmol/L at Bryce Canyon, 25.1 μmol/L at Green River). Sulfate was

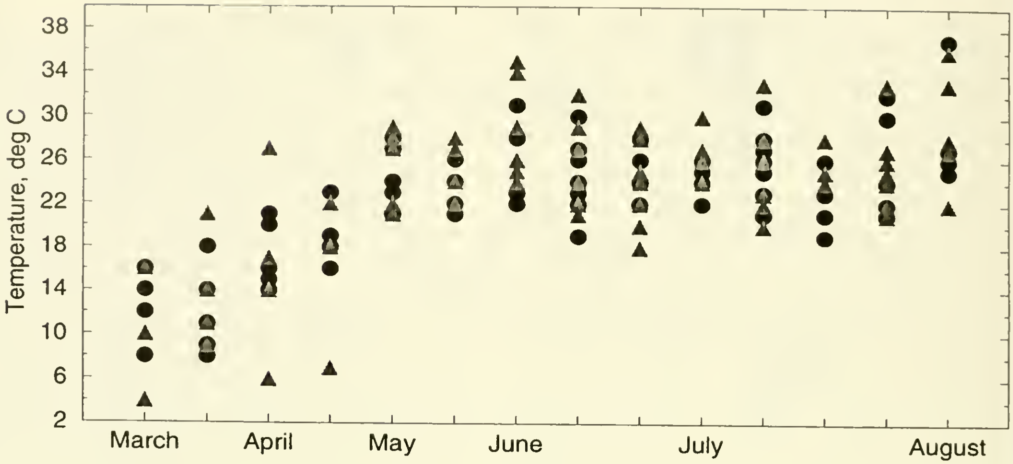

Fig. 3. Pool temperatures (°C) during the study period. Circles represent temperatures of pools with vegetated wetlands; triangles are pools surrounded by bedrock.

higher in Fountain Tanks, with a mean concentration of 38.5 µmol/L. Fountain Tanks is the southernmost set of pools for which we analyzed chemical composition and closest to regional industrial centers that are dominant sources of sulfur oxides in the region (Eatough et al. 1996). Although it is possible that higher sulfate values in Fountain Tanks are due to deposition, and that deposition certainly contributes to the solute load of the pools, it is more likely that a slight change in bedrock mineralogy is the source of solutes. The highest concentrations of alkalinity, Ca^{2+}, Na^{+}, Mg^{2+}, and Cl^{-}, of all pools sampled were found in Fountain Tanks, and this suggests the difference in water quality is due to different bedrock composition rather than deposition.

Fountain Tanks solutes were 2–3 times more concentrated than either Cottonwood or Muley Tanks (Table 1), except for the major plant nutrients potassium, nitrate, and phosphate. The mean pH of Fountain Tanks (7.6) was slightly higher than the pH of Cottonwood and Muley Tanks (7.0 and 7.3), and the difference was significant between Cottonwood and Fountain Tanks, but not between Fountain and Muley Tanks ($P = 0.01$). Similarly, chloride concentrations were slightly higher for Fountain Tanks, but significantly different only between Fountain and Cottonwood Tanks ($P = 0.03$). Ammonium was lower and less variable in Fountain Tanks than the other 2 drainages. Concentrations of all solutes in Cottonwood and Muley Tanks were not significantly different from each other, with the exception of dissolved organic carbon (DOC). DOC was significantly higher (10.6 mg C/L), and more variable, in Muley Tanks than in either of the other 2 drainages ($P = 0.01$). Concentrations of DOC averaged 6.3 and 4.3 for Cottonwood and Fountain Tanks, respectively.

There was no discernible seasonal pattern to solute concentrations with time over the summer (Fig. 4). Alkalinity and calcium became more concentrated in vegetated pools of Fountain Tanks during the summer, but a similar pattern did not occur in the unvegetated Fountain Tank pools, nor in pools of either of the other drainages. Dissolved organic carbon at Muley Tanks reached concentrations as high as 13.2 mg C/L, possibly because a small rainstorm flushed organic material into pools from the surrounding watershed. Ammonium and nitrate concentrations were highly variable through time, ranging from below detection limits to >80 µeq NH_4/L and 28 µeq NO_3/L. There was no significant difference in concentrations within each drainage between pools surrounded by rock or vegetation. A plot of conductance versus normalized pool volume, using all pools, exhibits a negative relationship (Fig. 5). Drying accounted for only 0.29% of the change in measured conductance for the entire data set, but there was variability by drainage. In Fountain Tanks 68% of conductance variability was explained by pool drying, while 30% and 27% were explainable for Muley and Cottonwood Tanks, respectively.

TABLE 1. Mean concentrations (and standard deviations) of major ions from 3 drainages of Capitol Reef National Park, Utah. Means with the same letter are not significantly different. Solutes are reported as μmol/L unless otherwise indicated.

	Cottonwood Tanks		Muley Tanks		Fountain Tanks	
Analyte	Mean (*s*)	Sig.	Mean (*s*)	Sig.	Mean (*s*)	Sig.
pH	7.0 (0.4)	A	7.3 (0.9)	A	7.6 (0.5)	B/A
Conductivity, μS/cm	52.5 (34.3)	A	62.1 (41.5)	A	114.8 (49.5)	B
Calcium	192.1 (157.2)	A	217.1 (152.2)	A	524.0 (279.4)	B
Magnesium	57.6 (41.2)	A	65.8 (49.4)	A	135.8 (61.7)	B
Sodium	17.4 (13.1)	A	17.4 (17.4)	A	34.8 (13.1)	B
Potassium	32.25 (23.0)	A	43.5 (38.4)	A	28.1 (15.3)	A
Ammonium	22.2 (33.3)	A	33.3 (44.4)	A	5.5 (11.1)	B
Chloride	16.9 (11.3)	A	19.7 (22.6)	A	31.0 (11.3)	B/A
Nitrate	4.8 (12.9)	A	4.8 (9.7)	A	6.5 (8.1)	A
Sulfate	21.9 (13.5)	A	27.1 (3.1)	A	38.5 (15.6)	B
Phosphate	below detection	A	below detection	A	below detection	A
Alkalinity	502.8 (436.0)	A	555.3 (458.4)	A	1226.8 (729.8)	B
Silica	13.3 (1.7)	A	8.3 (1.7)	A	23.3 (18.3)	B
DOC, mg C/L	6.3 (2.6)	A	10.6 (9.5)	B	4.3 (1.7)	A

Biological Characterization

In all pools sampled, 59 separate macroinvertebrate and vertebrate taxa were found (Table 2). These included fathead minnows (*Pimephales promelas* Rafinesque) in the lowest Miahana pool that terminates close to Hall's Creek, a stream in which this species is common. Anurans were represented by the spadefoot toad (*Scaphiopus intermontanus* Cope), canyon treefrog (*Hyla arenicolor* Cope), and 2 other toads, *Bufo woodhousei* Girard and *Bufo punctatus* Baird and Girard. The fairy shrimp (*Streptocephalus texanus* Packard) occurred in all pools. A snail, *Physella* sp., was observed in all drainages. The remainder of the taxa were arthropods, present in both larval and adult forms.

Larvae of the caddisfly *Limnephilus taloga* Ross were common throughout the winter and spring months, and larval activity was observed even under ice in January. The mayfly *Callibaetis pictus* (Eaton) was found as nymphs throughout spring, summer, and fall.

Aquatic beetles were well represented in all pools. The diverse assemblage included predaceous dytiscid diving beetles ranging in size from the minute *Liodessus affinus* (Say) to the larger *Dysticus* sp. Common hydrophilid water scavenger beetles included *Berosus punctatissimus* (LeConte) and *Tropisternus ellipticus* LeConte. These water scavenger beetles are predaceous as larvae but collector-gatherers as adults (Merritt and Cummins 1996).

Water bugs, Notonectidae and Corixidae, were common throughout the year. The crawling water bug family Naucoridae was also found in late summer. The neuston complex consisted of water striders *Aquarius remigis* (Say) and *Microvelia torquata* Champion, and the whirligig beetle *Gyrinus plicifer* LeConte. Dipterans were represented by a single species of tabanid, various common chironomids, and a few mosquito species. Dragonflies and damselflies were common, including *Aeshna* spp. and *Sympetrum obtrusum* (Hagen) (Table 2).

Most species in the pools are also common in other aquatic habitats of the Colorado Plateau. Small groups of predators dominate the communities, whose species all appear to be either extremely vagile in dispersal and colonization attributes or adapted to hydrologically fluctuating habitats, such as the anurans (Figs. 6a–c). Associations changed through the sampling period, primarily due to life history phenologies. Sixty-two percent of species found in the pools were predators, and each cluster was primarily composed of species considered predaceous. Thirty-four percent of the species were herbivorous collector/gatherers and scrapers, while the remainder were collector/filter feeders.

The proportion of juveniles in rock pools decreased throughout spring and summer (Fig.

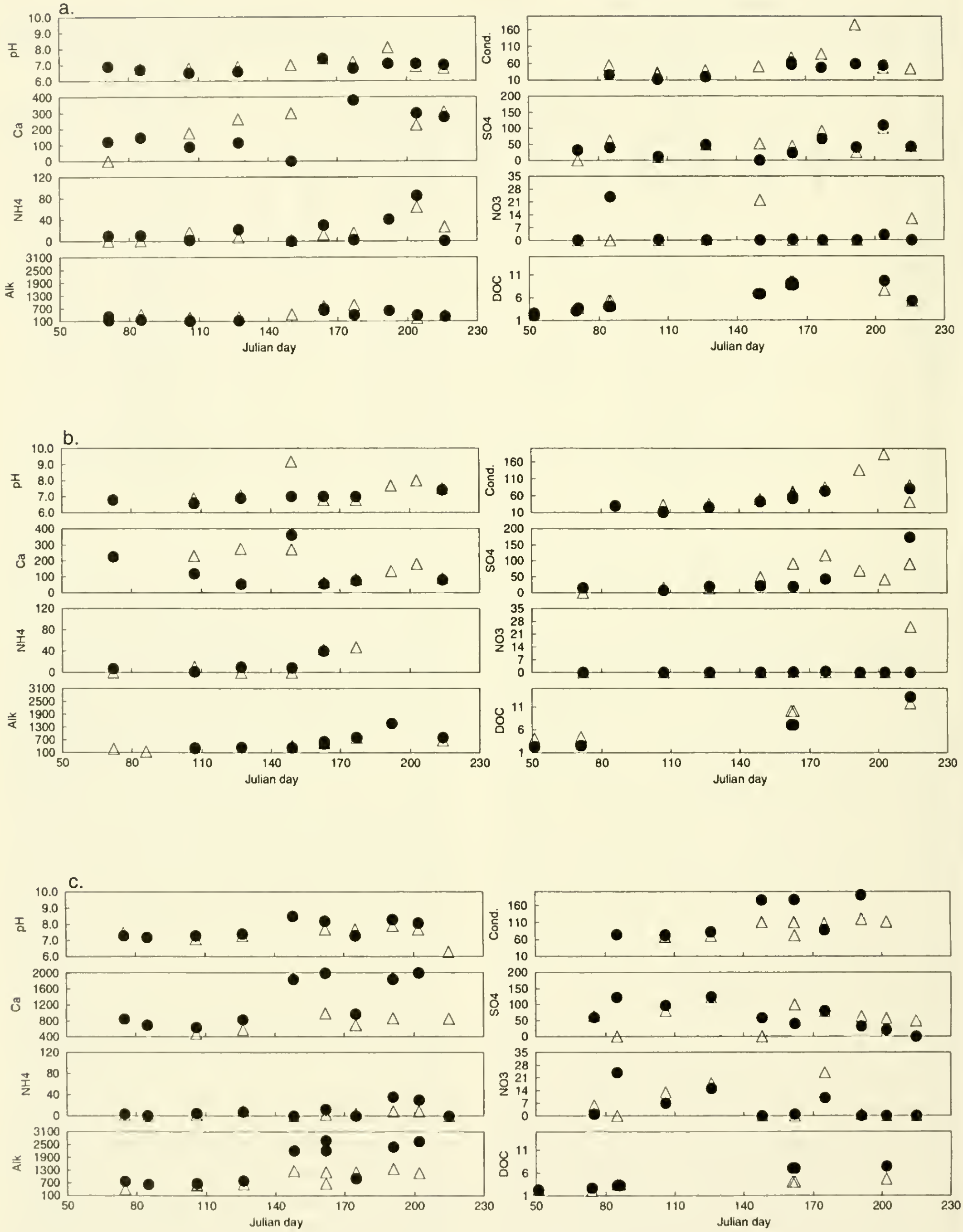

Fig. 4. Chemical dynamics of selected solutes over time in (a) Cottonwood Tanks, (b) Muley Tanks, and (c) Fountain Tanks. Solid circles represent pools with surrounding vegetation; open triangles are from unvegetated pools. Values for calcium (Ca), sulfate (SO_4), ammonium (NH_4), nitrate (NO_3), and alkalinity (Alk) are in µeq/L. Note difference in scale for Ca for Fountain Tanks. Specific conductance (Cond.) values are in µS/cm^2, and dissolved organic carbon (DOC) values are in mg C/L. Julian days are numbered days of year since day 1 on January 1.

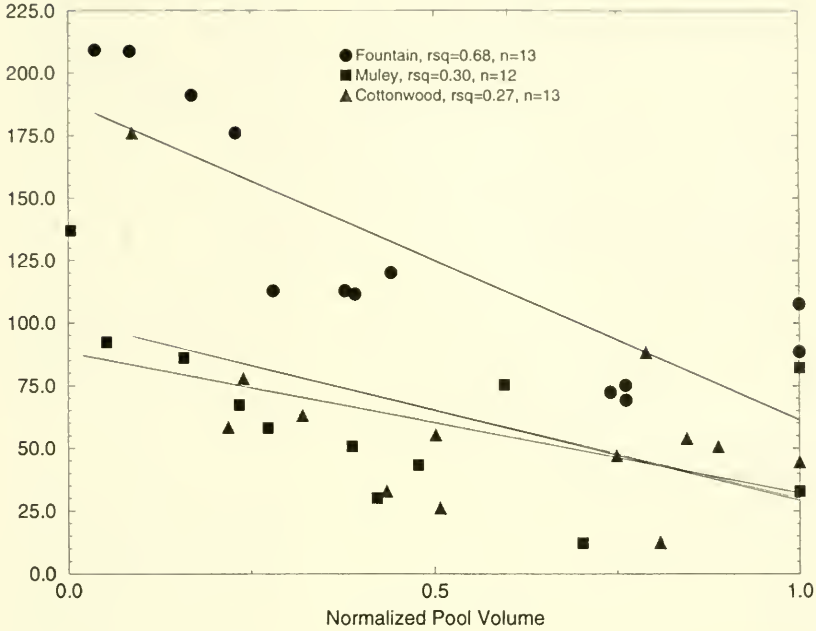

Fig. 5. Relationship of specific conductance (μS/cm^2) with normalized pool volume. Volume was normalized by dividing weekly volumes by the maximum pool volume measured during the study period.

7a), but there was no difference in the proportion of juvenile versus adult stages between pools with vegetation versus those surrounded by rock ($P = 0.586$). There were more species in pools that were components of vegetated wetlands (mean = 10.5, $s = 4.4$, $n = 116$) than pools situated in bedrock only (mean = 7.2, $s = 3.2$, $n = 116$), although numbers of species declined in both types of pools from spring through summer (Fig. 7b). Neither pool volume ($P = 0.54$) nor temperature ($P = 0.74$) affected the number of species present.

The effect of flooding on species numbers was not significant, either when comparing numbers of species within all pools before and after flood events ($P = 0.54$), or when rock-bordered pool species numbers were treated separately from those surrounded by vegetation ($P = 0.87$). Data were normalized by square root transformation. To eliminate the potential for autocorrelation, we did not use the 2 middle flooding events in Cottonwood drainage (see Fig. 2). The first and last storms were considered sufficiently separate events to satisfy conditions of independence.

A similar test was performed to examine the responses of pools to drying as a disturbance. Such disturbances were relatively infrequent (compared with pools studied by Dodson 1987). Pre-drying numbers of species and juvenile-to-adult ratios were tested against post-drying parameters directly after the first filling event. Both variables were normalized with square root transformations. Neither was significantly different as a result of drying (species numbers, $P = 0.16$; life history stage ratio, $P = 0.49$).

DISCUSSION

Communities found before and after both flooding and drying events were very similar, suggesting that hydrologic extremes do not constitute much of a stress on community composition. Close spatial association of the rock pools and high numbers of predators in small systems buffered variations in the community structure expected to result from physical disturbance or competition (McLachlan 1985, Schneider and Frost 1996). Summer storms affected only a few drainages at a time, and only a few study pools of significant volume dried completely during the hot, dry summer. This suggests that only a portion of the Waterpocket Fold aquatic community is ever displaced at a time, leaving undisturbed areas as a

TABLE 2. Species list of macroinvertebrate and vertebrate rock pool species collected 11 September 1993 to 23 September 1994, and 25 October 1995 in Capitol Reef National Park, Utah.

- VERTEBRATA
  - CYPRINIDAE
    - *Pimephales promelas* Rafinesque
  - **Anura**
    - *Scaphiopus intermontanus* (Cope)
    - *Bufo punctatus* Baird and Girard
    - *Bufo woodhousei* Girard
    - *Hyla arenicolor* Cope
- GASTROPODA
  - *Physella* sp.
- NEMATOMORPHA
- ARTHROPODA
  - **Class Anostraca**
    - *Streptocephalus texanus* Packard
  - **Class Conchostraca**
    - *Eulimnidia texana* Packard
  - **Class Nostostraca**
    - *Triops longicaudatus* (LeConte)
  - **Class Arachnida**
    - **Hydrachnida**
  - **Class Hexapoda**
    - **Collembola**
      - ISOTOMIDAE
    - **Ephemeroptera**
      - BAETIDAE
        - *Callibaetis pictus* (Eaton)
    - **Odonata**
      - AESHNIDAE
        - *Aeshna multicolor* Hagen
        - *Aeshna palmata* Hagen
        - *Anax junius* (Drury)
      - LIBELLULIDAE
        - *Sympetrum obtrusum* (Hagen)
        - *Libellula saturata* (Uhler)
      - LESTIDAE
        - *Archilestes grandis* (Rambur)
      - COENAGRIONIDAE
        - *Enallagma cyathigerum* (Charpentier)
        - *Argia* sp.
    - **Hemiptera**
      - NOTONECTIDAE
        - *Notonecta kirbyi* Hungerford
        - *Notonecta undulata* Say
        - *Buenoa margaritacea* Torre-Bueno
      - NAUCORIDAE
        - *Ambrysus mormon mormon* Montandon
      - GERRIDAE
        - *Aquarius remigis* (Say)
      - VELIIDAE
        - *Microvelia torquata* Champion
      - CORIXIDAE
        - *Graptocorixa abdominalis* (Say)
      - BELOSTOMATIDAE
        - *Lethocerus americanus* (Leidy)
    - **Trichoptera**
      - LIMNEPHILIDAE
        - *Limnephilus taloga* Ross
    - **Coleoptera**
      - GYRINIDAE
        - *Gyrinus plicifer* LeConte
      - HYDROPHILIDAE
        - *Hydrophilus triangularis* Say
        - *Tropisternus ellipticus* (LeConte)
        - *Hydrochara lineata* (LeConte)
        - *Berosus punctatissimus* LeConte
        - *Laccobius* sp.
      - DYTISCIDAE
        - *Agabus disintegratus* (Crotch)
        - *Agabus lugens* LeConte
        - *Agabus tristis* Aube
        - *Agabus semivittatus* LeConte
        - *Rhantus gutticollis* (Say)
        - *Laccophilus maculosus decipiens* LeConte
        - *Stictotarsus striatellus* (LeConte)
        - *Liodessus affinus* (Say)
        - *Neoclypeodytes discretus* (Sharp)
        - *Hygrotus collatus* (Fall)
        - *Thermonectus marmoratus marmoratus* (Hope)
        - *Uvarus subtilis* (LeConte)
        - *Dytiscus* sp.
      - HALIPLIDAE
        - *Peltodytes callosus* (LeConte)
    - **Diptera**
      - TABANIDAE
        - *Tabanus* sp.
      - CHIRONOMIDAE
        - *Chironomus* sp.
        - *Polypedilum* sp.
        - *Phaenopsectra dyari* (Townes)
        - *Phaenopsectra* sp.
        - *Micropsectra* sp.
        - *Alotanypus* sp.
      - CERATOPOGONIDAE
        - *Bezzia* sp.
      - CULICIDAE
        - *Anopheles fransiscanus* McCracken
        - *Culex tarsalis* Coquillett
        - *Culiseta inornata* (Williston)
        - *Culiseta* sp.

source of recovery. Many of the species we found were well adapted for rapid recolonization of pools after disturbance, having highly mobile adult stages, terrestrial adult mating and dispersal stages, or animal- or wind-dispersed eggs. Recolonization can also come from survivors or eggs laid prior to disturbance (Cushing and Gaines 1989). Pools that were components of vegetated wetlands supported greater numbers of species throughout the year, but none of these species occurred only in pools with vegetated wetlands. The lack of distinct species associations in the cluster analysis implies that all species occupied a similar ecological niche, which is likely the result of close ecological association, and proximity and

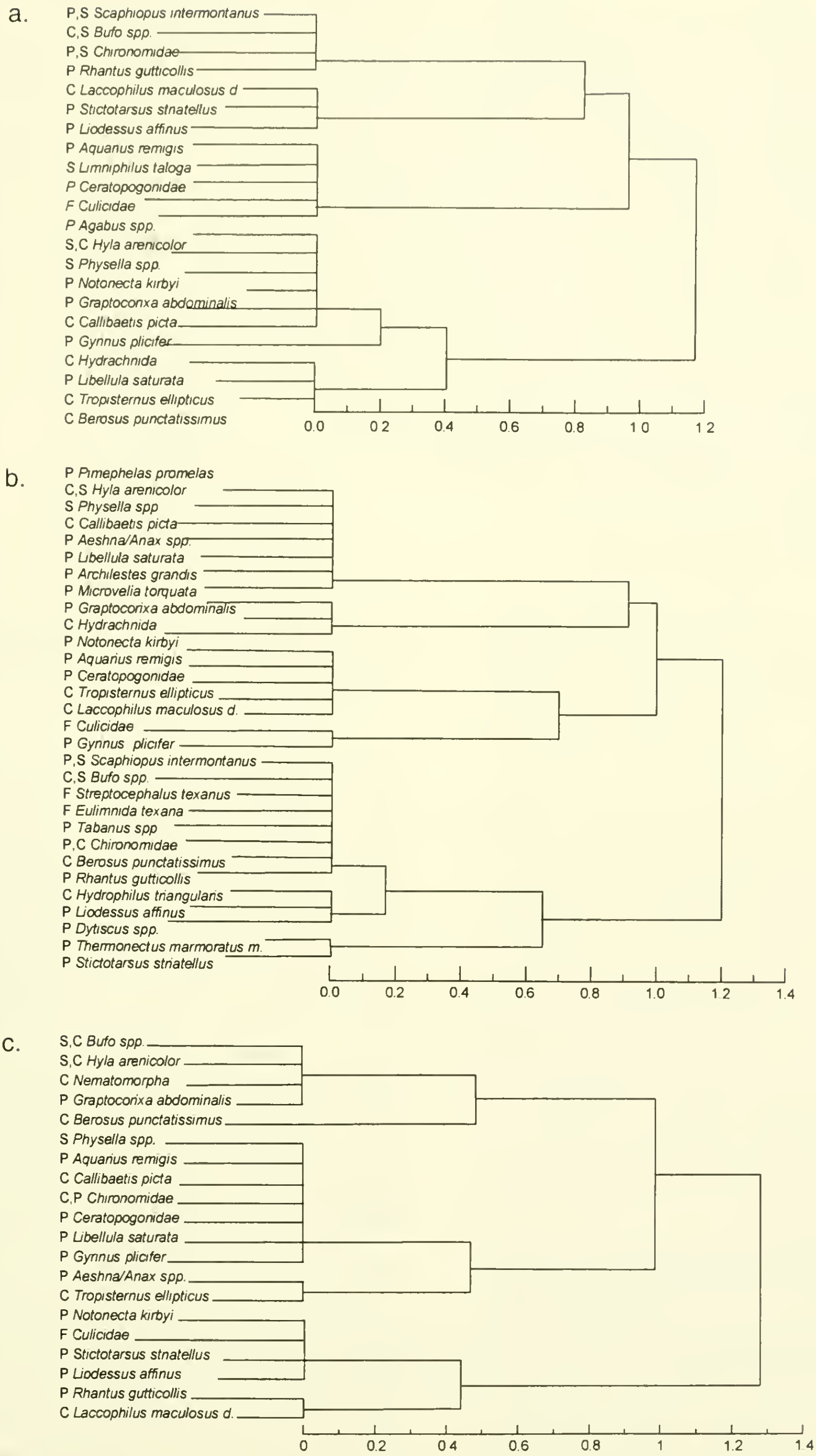

Fig. 6. Average linkage cluster analysis for aquatic species collected on (a) 15 March 1994, (b) 10 June 1994, and (c) 29 July 1994. Clusters are expressed as normalized root mean square distances. Species are annotated with functional feeding group after Merritt and Cummins 1996 as follows: P, predator; S, scraper; C, collector/gatherer; and F, filter feeder.

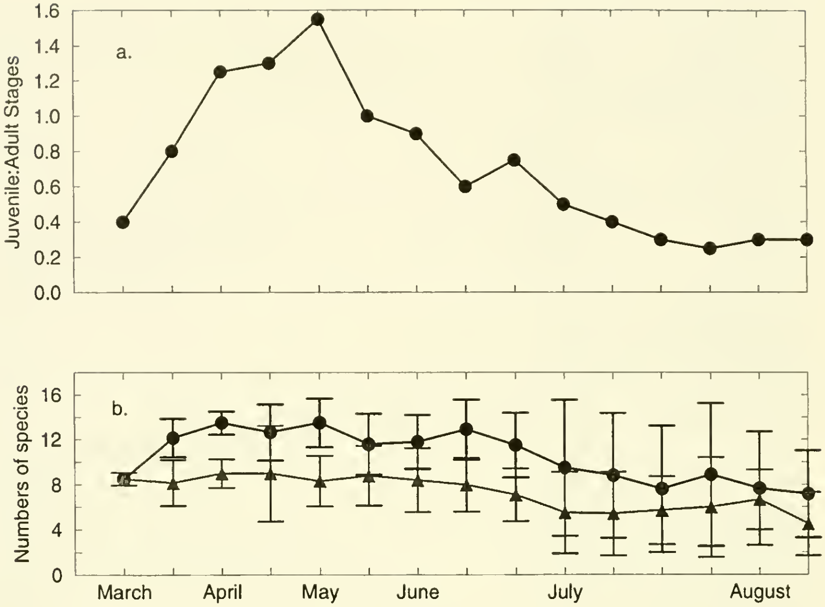

Fig. 7. Characteristics of aquatic organisms in Capitol Reef rock pools over time: (a) average ratio of juvenile to adult stages, and (b) species numbers. Circles are numbers in pools with vegetation, and triangles are numbers in pools surrounded by bedrock.

similarity of the rock pools. The alternative, which was not observed, would have shown persistent and distinct clusters of species.

The rapidity of recovery suggests these systems display great resilience, a conclusion also reached in a study of macroinvertebrate recovery after flash floods in Sycamore Creek, Arizona (Grimm and Fisher 1989). Flood events can introduce nutrients and detritus from precipitation and upstream as they wash debris and salts from upstream contributing areas (Creed et al. 1996). Grimm and Fisher (1989) hypothesize flood events are necessary to the maintenance of macroinvertebrate populations because they refresh the food supply for fast-growing organisms.

There was a chemical response to drying and flooding in the pools, although the strength of the response varied by solute and pool. It appears that nutrients and DOC increased after flood events, but salts became more concentrated with drying. Some chemical constituents, such as alkalinity, increased by an order of magnitude during the study period (concurrent with declining pool volume) but rapidly decreased after a rain event (Fig. 4). Pool chemistry was very dilute and was not significantly influenced by the presence or absence of vegetated wetlands.

In summary, rock pools of Capitol Reef National Park are populated with a fauna well adapted to survival in an environment of hydrologic extremes. The dilute chemical concentrations we measured did not vary broadly enough to pose a salinity problem for aquatic organisms. The ability of communities to recover after floods and droughts is consistent with a hypothesis posed by Hynes (1970) and results found by others (summarized by Cushing and Gaines 1989), that streams with flashy hydrology should have less abundant and less varied fauna than others. Cushing and Gaines (1989) developed a classification scheme for colonization and recolonization characteristics of different stream types. Capitol Reef rock pools fit well under the classification for exorheic cold desert streams in that the many small streams of the Waterpocket Fold provide colonization sources for each other. The diversity of stream and drainage habitats offers many pathways for faunal recovery, including downstream drift, upstream migration, both surface and hyporheic refugia in wetlands surrounding some pools, as well as adult and egg survivors of disturbances.

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SURVIVORSHIP AND CAUSE-SPECIFIC MORTALITY IN FIVE POPULATIONS OF MULE DEER

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ABSTRACT.—We used retrospective analyses to investigate cause-specific mortality and survivorship among 5 populations of mule deer (N = 168 telemetered animals) wintering in the western Great Basin during 1986–1994. These populations existed under similar environmental conditions, but survivorship functions differed among them. Monthly survival ranged from 0.964 to 0.990, and annual survival ranged from 0.643 to 0.884. The proportion of deaths attributed to predation and malnutrition or anthropogenic causes did not differ among the 5 populations. Predation was the leading cause of mortality; mountain lions were responsible for approximately 90% of the deer killed by predators. No difference existed among these populations in the proportion of telemetered deer that were killed by mountain lions, but proportionally more females than males were killed by these large felids. Predation by mountain lions is the primary source of mortality and a widespread phenomenon among the populations of mule deer we investigated.

Key words: California, Felis concolor, Odocoileus hemionus, *mule deer, mortality, mountain lion, predation, survivorship.*

Populations of mule deer (*Odocoileus hemionus*) have been declining in western North America for many years (Workman and Low 1976), and effects of nutrients, competition, predation, and climate on these populations have been debated among numerous investigators. Mule deer are thought to be density dependent in their response to resource availability (McCullough 1990). In unpredictable environments (typical of much of the Great Basin), however, it may be difficult to base management recommendations on density-dependent responses anticipated to follow population declines (Mackie et al. 1990). Whatever factors, singularly or in combination, regulate mule deer populations remain open to discussion. Indeed, there is general agreement that no single cause can be invoked. Detailed and specific investigations are necessary to evaluate factors that may regulate populations of these important game animals (Hornocker 1976, Knowlton 1976, Connolly 1981).

Recently, Wertz (1996) expressed concern about the dynamics of several mule deer populations wintering in the western Great Basin. Highway mortality has been a basis for this concern, as have the effects of predation and disease. Persistent drought has lowered the carrying capacity of deer winter ranges in this general area, with resultant negative influences on the physical condition of these large herbivores (Kucera 1988, Taylor 1996). Moreover, the harsh winter of 1992–93 killed many deer, particularly in northeastern California and northwestern Nevada (Wertz 1996).

To better understand factors affecting deer populations in the western Great Basin, we investigated seasonal distribution, habitat selection, cause-specific mortality, and survivorship in 5 populations of mule deer wintering in eastern California and western Nevada. In this paper we use retrospective analyses based on telemetered animals (White and Garrot 1990) to compare cause-specific mortality among 5 mule deer populations that winter in the western Great Basin. Additionally, we describe and compare survivorship functions for female deer in these populations.

DESCRIPTION OF THE STUDY AREA

Our study area is located in Mono and Inyo counties, California, and Douglas County, Nevada (Fig. 1). Deer from the West Walker, East Walker, Mono Lake, and Casa Diablo winter ranges are migratory and display annual patterns of movement and range use. In spring they make long-distance movements, sometimes >60 km, and spend summers on both the east and west slopes of the Sierra Nevada

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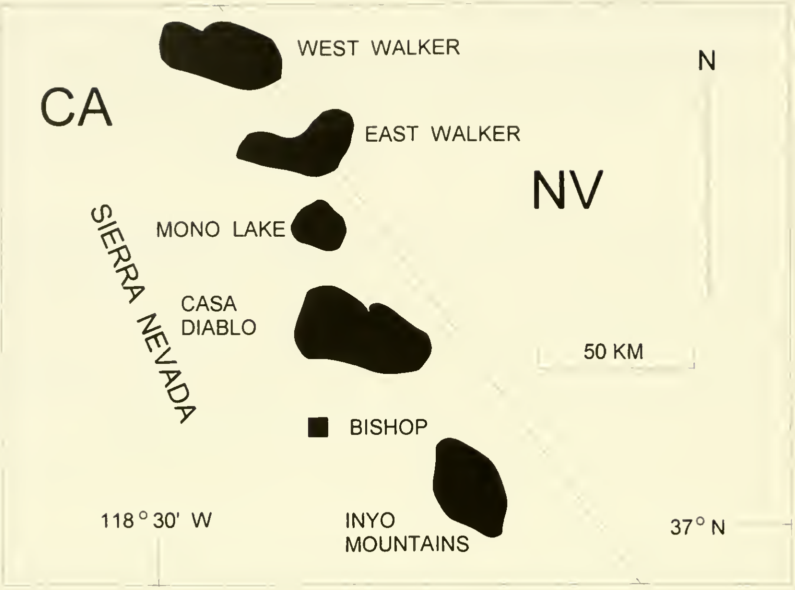

Fig. 1. Location of 5 winter ranges in northeastern California and western Nevada. Mule deer concentrate on these areas from approximately 1 November to 15 May each year.

(Taylor 1988, 1991). During autumn deer from these populations return to discrete winter ranges on the western edge of the Great Basin, where they remain from about 1 November to 15 May (Taylor 1988, 1991). Deer inhabiting the Inyo Mountains undergo altitudinal migrations similar to those described by Nicholson et al. (1997), but generally do not exhibit the extensive movements made by deer from the other 4 populations. Currently, 4 of the populations (West Walker, East Walker, Mono Lake, Casa Diablo) are classified as Rocky Mountain mule deer (*O. h. hemionus*); deer occupying the Inyo Mountains are classified as Inyo mule deer (*O. h. inyoensis*), a taxon of questionable validity (Wallmo 1981, Cronin and Bleich 1995).

During winter all 5 populations of deer occur largely in sagebrush (*Artemisia tridentata*) steppe or pinyon pine (*Pinus monophylla*) habitat, ranging in elevation from 1500 m to 2300 m (Taylor 1988, 1991, V.C. Bleich and D. Racine unpublished data). The primary winter forage for the 4 northern populations is bitterbrush (*Purshia* spp.; Taylor 1988, 1991). Although bitterbrush occurs in the Inyo Mountains (DeDecker 1991), specific data on deer diets in that range are lacking.

The Sierra Nevada creates a formidable rain shadow, and during winter these deer occupy an arid region with low and unpredictable precipitation (Fig. 2), similar to that described by Kucera (1988). Since 1986, the Great Basin immediately east of the Sierra Nevada has experienced repeated annual droughts; as a result, ecological carrying capacity of many winter ranges has declined (Taylor 1991). Migratory populations of mule deer can be substantially affected by drought conditions on winter ranges despite adequate forage during summer (Kucera 1988). During years of low precipitation, bitterbrush production is poor and deer subsist on suboptimal diets consisting largely of conifers, sagebrush, and blackbrush (*Coleogyne ramosissima;* Kucera 1988, Taylor 1991).

Methods

During 1986–1991, we used Clover (1956) traps, a helicopter and linear drive nets (Thomas and Novak 1991), and a hand-held net gun fired from a helicopter (Krausman et al. 1985) to capture mule deer. We fitted adult (≥1-yr-old) animals with color-coded ear tags and telemetry collars (Model 500, Telonics, Inc., Mesa, AZ) that incorporated a mortality sensor with a 6-h delay. We collared each animal at its capture site and released it when processing was completed. By distributing our

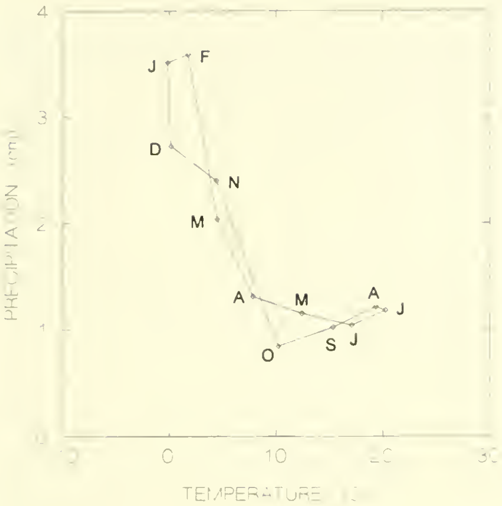

Fig. 2. Climate throughout the study area typically is cold during winter and hot during summer. Precipitation occurs primarily as snowfall during winter, but variance in annual precipitation is high. The climograph was developed from data obtained 1961–1990 from the Western Regional Climate Center using the mean of monthly mean values of minimum and maximum temperatures for Bishop, Bridgeport, Bodie, and Independence, California.

capture efforts throughout all winter ranges, we minimized potential biases associated with heterogeneous use of those areas by deer. We collared male and female deer in the approximate proportion of their occurrence in each population. Each winter, we used ground-based chemical immobilization or a helicopter and net gun to capture and radio-collar additional deer in each population.

In the 4 northern populations, we used aerial and ground telemetry to monitor the status of deer at intervals ≤1 wk; thus, date of death could be closely estimated. Using only aerial telemetry in the Inyo Mountains, we monitored those deer at approximately 2-wk intervals. For animals for which we could not ascertain the date of death, we assumed death occurred midway between the last known live observation and the date on which a mortality signal was first received.

We attempted to determine the cause of mortality for every deer that died. For animals killed by predators, we used the criteria of Shaw (1983) and Woolsey (1985) to identify the species of predator in all but one instance. Nutritional status was indexed by condition of marrow in long bones (Cheatum 1949). When we could not ascertain the source of mortality, we listed the cause of death as undetermined. G-tests were used for categorical analyses, and a binomial test compared the proportion of deer killed by mountain lions during different years (Zar 1984).

We used the Kaplan-Meier (1958) estimator, as modified by Pollock et al. (1989), for staggered entry of telemetered females into each population, and determined survivorship on a monthly basis. To compare survivorship functions, we used the log-rank test (Cox and Oakes 1984) as modified by Pollock et al. (1989). We calculated the most conservative chi-square statistic presented by Pollock et al. (1989) to enhance the probability that any differences detected between survivorship functions were real.

Survivorship was not evaluated on all winter ranges concurrently, and deer were not initially collared at the same time of year. To minimize seasonal effects on mortality in this retrospective analysis, we compared survivorship of females from paired populations from the beginning of the 1st April during which collared deer from each population pair were available to the end of the period for which paired monthly data were available for those particular populations. For example, we studied cause-specific mortality in the West Walker population during April 1992–January 1995, and in the Inyo Mountains population during October 1991–December 1994; for this pair, comparisons of survivorship curves spanned a period of 2 yr and 9 mon, from 1 April in year 1 to 31 December in year 3. Using this method, we compared survivorship over periods of 21 mon for 4 pairs of populations, and over 27 mon for 5 other pairs. To facilitate comparisons, we also calculated finite, annual, and monthly survivorship for females in each population. We restricted our analyses to females because the genders of sexually dimorphic ungulates may occupy different habitats, experience different risks of natural mortality (Bleich et al. 1997), and respond differently to the threat of predation (Bleich in press).

We collected data for a minimum of 24 mon in the Casa Diablo population and a maximum of 39 mon in the Inyo Mountains. Although the investigations did not all run concurrently, these 5 populations occupy similar habitats in close proximity to each other, they were exposed to similar climatic regimes (Table 1),

TABLE 1. Correlation matrices for climatological data obtained 1961–1990 from the Western Regional Climate Center for Bishop, Bridgeport, Bodie, and Independence, California. These stations are all located on or near the winter ranges investigated herein.

	Average monthly maximum temperature			
	Bishop	Bodie	Bridgeport	Independence
Bishop	1.000	0.988	0.995	1.000
Bodie	0.996	1.000	0.995	0.987
Bridgeport	0.996	0.997	1.000	0.995
Independence	0.999	0.997	0.995	1.000
	Bishop	Bodie	Bridgeport	Independence
	Average monthly minimum temperature			

	Average monthly precipitation			
	Bishop	Bodie	Bridgeport	Independence
Bishop	1.000	0.936	0.972	0.996
Bodie		1.000	0.934	0.935
Bridgeport			1.000	0.979
Independence				1.000

and several of the investigations were ongoing simultaneously. Thus, we assumed that qualitative differences among these winter ranges were minimal.

RESULTS

We radio-collared 168 adult mule deer (27 males, 141 females) and monitored them for 21–39 mon (2829 telemetry-months; Table 2). We determined the proximate source of mortality for 76% of the females (41 of 54) and 85% of males (11 of 13) that died. Among females, confirmed causes of death ranged from 57% in the Inyo Mountains to 100% in the East Walker population. Among the 41 mortalities of females for which the cause of death is known, 83% were attributed to predation, 4.8% were human-induced, and 12.2% were due to malnutrition. In the northernmost population (West Walker), 3 of 10 mortalities resulting from predation occurred during or immediately after the severe winter of 1992–93, and 7 of 10 occurred during or following the mild winter of 1993–94 ($P > 0.10$). Among males that died, predation by mountain lions accounted for 36% and hunting for 64% of the 11 mortalities for which the cause of death was determined; the source of mortality for 2 males could not be ascertained. We detected no evidence of malnutrition among animals killed by predators or among those dying of anthropogenic causes.

Predation accounted for >70% of the known causes of death for females on each winter range (Fig. 3). The proportion of deaths attributed to predation did not differ among these populations ($G = 5.987$, df = 4, $P = 0.200$) when human-induced mortality and malnutrition were pooled. For males, sample sizes were too small to allow a comparison among populations.

Of 34 female mule deer killed by predators, mountain lions accounted for 91% of the deaths (Fig. 4). No difference existed among the 5 populations in the proportion of females killed by mountain lions ($G = 2.979$, df = 4, $P = 0.561$). Overall, the proportion of female deer whose deaths were attributable to predation by mountain lions (31 of 41) was significantly greater than the proportion of males killed by these large felids (4 of 11; $G = 5.751$, df = 1, $P = 0.016$).

Survivorship functions of female deer differed significantly for 3 of 10 pairwise comparisons (Table 3). Survivorship for the West Walker population differed from the Mono Lake, Inyo Mountains, and East Walker populations, and was marginally nonsignificant for the Casa Diablo population. The finite survival

TABLE 2. Sample sizes and estimates of monthly and annual survivorship for West Walker (WW), Casa Diablo (CD), East Walker (EW), Mono Lake (ML), and Inyo Mountains (IM) mule deer populations, Inyo and Mono counties, California, and Douglas County, Nevada, 1986–1994.

Winter range[a]	Deer (N)	Telemetry-months (N)	Monthly survivorship	$s_{\bar{x}}$	Annual survivorship	$s_{\bar{x}}$
WW	48	823	0.964	0.004	0.643	0.010
CD	27	469	0.985	0.004	0.837	0.014
EW	23	428	0.990	0.004	0.884	0.014
ML	23	512	0.979	0.006	0.777	0.018
IM	20	597	0.973	0.008	0.717	0.022

[a] Inclusive dates of each investigation were WW, April 1992–January 1995; CD, January 1986–December 1987; EW, March 1988–June 1990; ML, March 1988–June 1990; IM, October 1991–December 1994.

rate among these populations ranged from about 0.75 in the East Walker population to about 0.30 in the West Walker population, which had the highest proportion of mortality caused by malnutrition. Among these populations monthly survival estimates ranged from 0.964 to 0.990, and annual survival estimates ranged from 0.643 to 0.884 (Table 2). Too few males were marked to allow a meaningful estimate of survivorship for males occurring in these populations.

DISCUSSION

Predation was the most common cause of mortality among 5 mule deer populations that winter east of the Sierra Nevada (Fig. 3). Human-induced mortality and malnutrition varied among these populations. Based on our analyses, we conclude that sources of mortality were similar among these winter ranges for the periods we studied. Deaths of female deer resulting from human activities were recorded only in the West Walker and Casa Diablo populations. Death resulting from malnutrition was restricted to the West Walker and Mono Lake populations and accounted for 25% and 21% of the mortality in those populations, respectively. Malnutrition overall (9.8%) was, however, not an important cause of death.

Among deer killed by carnivores, mountain lions were the most common predator, and no differences existed in the proportion of female deer killed by mountain lions among the 5 populations we investigated (Fig. 4). Our findings are consistent with previous ones that mule deer are important prey of mountain lions throughout western North America (Hornocker 1976, Russell 1978). Proportionally more telemetered females than males were killed, suggesting that females may be more vulnerable to predation by mountain lions.

There was a difference in survivorship functions between 3 of 10 pairs of populations that we compared (Table 3), and the results were but marginally nonsignificant for a 4th pair. Small samples possibly influenced our ability to detect differences (Pollock et al. 1989) between other population pairs, but the magnitude of differences between 6 pairs, when compared to the remaining 4, suggests sample size was not problematic (Table 3). These findings were somewhat unexpected given the physical, climatological, vegetational, and faunal similarities among the winter ranges we examined, and may be attributable to the high proportion of mortality from malnutrition in the West Walker population during the winter of 1992–93; that winter was especially severe in northeastern California (Wertz 1996).

In none of our study populations are historical demography and habitat quality adequately known to begin to factor out the relative roles of nutrition, predation, and climate as factors influencing the dynamics of these populations. Additionally, the effects of these factors on survival of young <1 yr old were not investigated. With the exception of the Mono Lake and West Walker populations, the absence of animals dying of malnutrition suggests that mortality from predation generally was not compensatory. Many female deer collected from the West Walker winter range were in poor physical condition following the winter of 1992–93 (Taylor 1996), and some animals in that population may have been predisposed to death by predation during our investigation. Nevertheless, only 3 of 10 animals killed by predators in the West Walker population died that winter, but 7 of 10 were killed during the mild winter of 1993–94. Despite the deaths of 2 females from malnutrition in the Mono Lake population, individuals there were in much better condition than were West Walker females

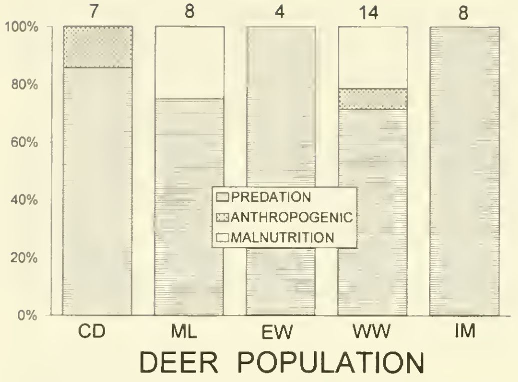

Fig. 3. Proportion of mortalities ($N = 41$) of female deer that can be attributed to predation, anthropogenic causes, and malnutrition in each of 5 deer populations inhabiting eastern California and western Nevada, 1986–1994. Numbers above each bar are total mortalities from known causes for each population; CD = Casa Diablo, EW = East Walker, ML = Mono Lake, WW = West Walker, and IM = Inyo Mountains.

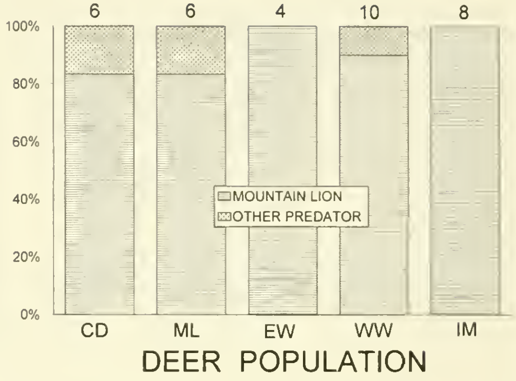

Fig. 4. Proportion of predation on female deer attributed to mountain lions and other predators in each of 5 deer populations studied in eastern California and western Nevada, 1986–1994. Numbers above each bar represent total mortality attributed to predators for each population; CD = Casa Diablo, EW = East Walker, ML = Mono Lake, WW = West Walker, and IM = Inyo Mountains.

during 1992–93 (Taylor 1991). Body condition of Mono Lake females during the period they were under study approached that of the West Walker population during 1994, a year when no animals died of malnutrition. None of the animals killed by predators exhibited evidence of depleted fat reserves upon examination of femur marrow. If malnutrition was an important factor predisposing individuals to death by other causes, we would have expected to find evidence of such among victims of predation or human-induced mortality; this was not the case.

The role of predation in regulating populations of large mammals remains open to debate (Skogland 1991), and predation as a factor potentially regulating deer populations has not been widely accepted (Connolly 1981). For example, the effects of mountain lion predation have been described as unimportant (Janz and Hatter 1986) and conversely as having strong local effects (McNay and Voller 1995) on deer occurring in the same geographic area. These large felids were responsible for most mortality of adult female deer in each of the populations we investigated. Although we noted few adults killed by coyotes (*Canis latrans*), these canids can have important effects on deer population dynamics, especially through their influence on fawn survival (Knowlton 1976, Bowyer 1987).

Predation may warrant special consideration as a factor in the dynamics of mule deer occupying unpredictable environments. Indeed, investigations in boreal systems have suggested that predation by wolves (*Canis lupus*) and bears (*Ursus* spp.) can preclude recovery of large mammal populations that have become depressed by a single source, or a combination of several sources, of mortality (Gasaway et al. 1983, 1992, Van Ballenberghe 1987). Based on observations in the Sierra Nevada, Wehausen (1996) suggested that predation by mountain lions has substantially influenced the population dynamics of mountain sheep in part of the western Great Basin. Removal of several mountain lions was necessary to preclude the extirpation of one population of these specialized ungulates (Bleich et al. 1991), and that population of mountain sheep is sympatric with the Casa Diablo deer population for part of the year (Taylor 1991).

Given the similarities in cause-specific mortality and the importance of predation as a cause of death among the populations we studied, the potential for predation to regulate deer populations might be reconsidered and further investigated, particularly for migratory deer inhabiting the arid, unpredictable ecosystems typical of the western Great Basin. In such systems predation clearly is an important source of mortality and may assume greater importance

TABLE 3. Pairwise comparisons of survivorship functions for West Walker (WW), Casa Diablo (CD), East Walker (EW), Mono Lake (ML), and Inyo Mountains (IM) mule deer populations, Inyo and Mono counties, California, and Douglas County, Nevada, 1986–1994. Chi-square statistics are shown above the diagonal; probabilities that survivorship functions did not differ are shown below the diagonal. For all comparisons, degrees of freedom = 1.

	Chi-square values				
Population	WW	EW	ML	CD	IM
WW	——	7.611	4.235	2.458	4.977
EW	<0.01	——	0.388	0.326	0.231
ML	<0.05	>0.50	——	0.248	0.130
CD	>0.10	>0.50	>0.50	——	0.012
IM	<0.05	>0.50	>0.50	>0.90	——
	Probability that survivorship did not differ				

in population limitation than in more mesic environments where the effects of climate are more tempered and more predictable.

In highly variable systems, density-independent events (i.e., droughts and harsh winters) occur unpredictably (Mackie et al. 1990) and can result in unanticipated population declines that confound conservation strategies. Nonetheless, density dependence would continue to operate (McCullough 1990) in such systems and could indirectly affect predation rates (McCullough 1979). Only through carefully designed, long-term investigations, however, will it be possible to reach meaningful conclusions regarding effects of predation and other sources of mortality on populations of migratory deer occupying Great Basin ecosystems.

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PERSISTENCE OF SUBALPINE FOREST–MEADOW ECOTONES IN THE GUNNISON BASIN, COLORADO

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ABSTRACT.—Forests of the southern Rocky Mountains are punctuated by persistent meadows called parks that are dominated by grasses and forbs. In an attempt to elucidate the maintenance of subalpine parks in the Gunnison Basin, Colorado, soil texture and tree morphology differences along 60-m transects spanning the forest-park ecotone were studied in 6 representative parks. Seedling survivorship, percent seed germination, and soil moisture available to plants were also studied along one of the transects in Willow Park. Soil analyses revealed 40% more silt and significantly less sand and clay in all 6 parks ($P < 0.001$), which supports the traditional hypothesis that edaphic factors are involved in restricting establishment of trees in parks. In Willow Park moisture available to plants in soils at field capacity varied significantly across the ecotone ($P = 0.011$), with 54% more water in forest than in park soils. Measures of growth rate obtained from tree height, dbh, and age were significantly higher nearer the ecotone ($P < 0.001$). The coefficient of variation of annual-ring width was significantly higher in forest than in ecotone trees ($P = 0.002$). These results suggest that stress of mature Engelmann spruce (*Picea engelmannii*) and lodgepole pine (*Pinus contorta*) is an unlikely explanation of park maintenance. *P. engelmannii* percent seed germination and seedling survivorship were significantly higher in the forest than in the park ($P < 0.001$). This may be largely due to the more severe seedling microclimate observed in the park. Results indicate that limited seedling establishment is primarily responsible for maintenance of subalpine parks in the Gunnison Basin.

Key words: park, subalpine meadow, forest-meadow ecotones, Picea engelmannii, *soil texture, seedling establishment, seed germination, soil moisture, Gunnison Basin, Colorado.*

Montane and subalpine forests of the southern Rocky Mountains are punctuated with meadows dominated by grasses and forbs and varying amounts of sage (*Artemisia* spp.), willow (*Salix* spp.), and sedge (*Carex* spp.). Locally these treeless areas are called parks and range from <1 ha to thousands of hectares in size. In Colorado, parks form ecotones with ponderosa pine (*Pinus ponderosa*) forests in the montane zone and mainly lodgepole pine (*Pinus contorta*), Colorado blue spruce (*Picea pungens*), and Engelmann spruce (*Picea engelmannii*) forests in the subalpine zone.

Explanations for the presence of parks are numerous, but many are not supported by empirical evidence. Severe disturbances such as fires and logging may allow the initial formation of parks (Daubenmire 1943, Kuramoto and Bliss 1970, Koterba and Habeck 1971, Vale 1981, Lynch 1995). Once established, they may be maintained by a number of biotic and abiotic factors that may prevent the survival of mature trees, but more frequently cited is the prevention of seedling establishment (Klikoff 1965, Moir 1967, Dunwiddie 1977, Taylor 1990, Doering and Reider 1992, Woodward et al. 1995). Herbivory (Klikoff 1965, Noble and Shepperd 1973, Vale 1981, Cantor and Whitham 1989) and seedling competition with herbaceous vegetation (Robbins 1918, Peet 1988, Coates et al. 1991, Comeau et al. 1993, Burton and Bazzaz 1995) may be more prevalent in meadows than in neighboring forests. Adverse climatic conditions, such as more extreme temperature fluctuations, may also limit seedling establishment in parks (Pearson 1913, Kuramoto and Bliss 1970, Franklin et al. 1971, Taylor 1990, 1995, Lynch 1995, Woodward et al. 1995). However, if these were the only factors involved, tree invasion into parks would be expected as a result of enhanced seedling survival in the more mesic environment near the ecotone (Daubenmire 1943).

A commonly cited factor for the maintenance of forest-meadow ecotones is soil texture (Robbins and Dodds 1908, Pearson 1913, Dunnewald 1930, Ives 1942, Daubenmire 1943, Peet 1981, Veblen and Lorenz 1986, Doering and Reider 1992). Unlike other proposed explanations, which include factors that are moderated at the ecotone, soil texture is not readily modified by the forest. Thus, soil texture differences between forest and park may be capable of preventing tree encroachment. Daubenmire (1943) concluded that conifers of the Rocky Mountain region are adversely affected by some factor associated with fine-textured, compact, or poorly drained soils. Fine-textured soil may impede root elongation, preventing the seedling root from reaching subsurface moisture in a timely fashion (Daubenmire 1943, Patten 1963). Fine-textured soil may also retain soil moisture at higher tensions, thus decreasing soil moisture available to plants (Patten 1963). However, excessive drainage due to coarse-textured soil has been suggested by Pearson (1913) as a limiting factor in Arizona parks.

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Parks are frequent at 2700–3500 m elevation within the Gunnison Basin, Colorado. Park ecotones with *P. contorta* forests and *P. engelmannii* forests are most common, but quaking aspen (*Populus tremuloides*) also appear regularly throughout the basin. The purpose of our study was to elucidate the persistence of parks in the Gunnison Basin by examining suggested explanations of park maintenance. The 1st objective was to ascertain whether established trees at coniferous forest–park ecotones are stressed compared with trees in the forest interior. Such stress would suggest that limiting factors are operating on mature trees, and such factors may limit tree advance into parks. Stress would not be expected if parks are primarily the result of inhibited seedling establishment. The 2nd objective was to document *P. engelmannii* seed germination rates and seedling survivorship across the forest-park ecotone. Inhibited germination and reduced survivorship would be expected if limited tree establishment is maintaining parks. The 3rd objective was to document soil-texture and water-holding characteristics across coniferous forest–park ecotones. The presence of soil-texture gradients across park boundaries would support the contention that edaphic factors have a role in maintaining parks in the Gunnison Basin.

MATERIALS AND METHODS

Study Sites

We selected 6 parks to represent the diversity of coniferous forest–park ecotones in the Gunnison Basin (Fig. 1, Table 1). Two transects spanning the forest-park ecotone were established in each park. Transects were located in more pristine areas away from obvious disturbance and human activities. These 60-m transects were oriented perpendicular to the ecotone boundary and extended 30 m into the forest and 30 m into the park. Sampling occurred at the ecotone (0 m) and at 15 m and 30 m into both the forest and park. We randomly chose 3 soil sampling sites along a 30-m line oriented parallel to the ecotone at each of these distances. Similarly, we chose 3 trees at 0 m, 15 m, and 30 m into the forest to obtain tree-growth measurements for stress analysis. One transect in Willow Park was utilized to acquire data on seed germination, survivorship of 3-yr-old *P. engelmannii* seedlings, seedling microclimate regimes, and moisture available to plants in soils at field capacity.

Tree Morphology

Reduced tree growth, or stunting, was used to measure relative tree stress. Tree-growth parameters of 3 randomly selected trees were measured along the transects in all 6 parks at the ecotone (0 m) and at 15 m and 30 m into the forest. The diameter-at-breast-height (dbh) and height of each tree were measured, and each tree was cored at breast height using a Swedish increment borer oriented perpendicular to the slope. Cores were treated and analyzed according to Fritts (1976), yielding tree age and average annual-ring width. Stunting was discerned by lower height:age, dbh:age, and height:dbh ratios or narrower age-adjusted average annual-ring widths. Increased tree stress may also be indicated by a higher coefficient of variation resulting from greater sensitivity to climatic variation. The coefficient of variation (standard deviation divided by the mean) of tree-ring width was calculated using the age-adjusted average annual-ring widths for the last 10 yr (1983–1992). For each growth parameter (dependent variable), we used a nested ANOVA (transects nested within parks) to test the null hypothesis that location along the transect (proximity to the ecotone) has no effect on tree growth.

Seedling Establishment

To document the influence of the park environment on seed germination and establishment, we located three 40-m rows, oriented

TABLE 1. Descriptive summary of the 6 representative parks in the Gunnison Basin, Colorado.

Park	Latitude and longitude	Elevation (m)	Size (ha)	Soil parent material	Dominant forest species
Big Willow	38°14′N, 107°20′W	3450	160	basalts, tuffs, volcanic conglomerates	*Picea engelmannii*
Blue	38°06′N, 106°52′W	3328	370	ash flow tuffs	*Picea engelmannii*
Porphyry	38°29′N, 106°21′W	3280	15	granites	*Picea engelmannii* and *Pinus contorta*
Taylor	38°50′N, 106°35′W	2938	4110	glacial and outwash deposits	*Pinus contorta*
Union	38°47′N, 106°33′W	2987	800	granites	*Pinus contorta*
Willow	38°04′N, 106°55′W	3475	60	andesites, welded tuffs	*Picea engelmannii*

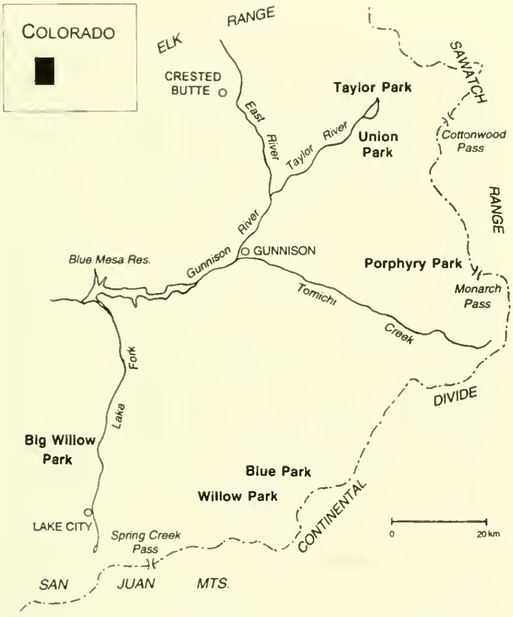
COLORADO
ELK RANGE
CRESTED BUTTE
East River
Taylor Park
Taylor River
Union Park
SAWATCH RANGE
Cottonwood Pass
Gunnison River
GUNNISON
Blue Mesa Res.
Porphyry Park
Tomichi Creek
Monarch Pass
Lake Fork
Big Willow Park
DIVIDE
Blue Park
Willow Park
CONTINENTAL
LAKE CITY
Spring Creek Pass
0
20 km
SAN JUAN MTS.

Fig. 1. Location of the 6 representative parks within the Gunnison Basin, Colorado.

parallel to the ecotone, in Willow Park at 30 m into the forest, at the ecotone (0 m), and at 30 m into the park. At 1-m intervals along the rows, we established 0.5 × 1.0-m seedbed grids, divided into 50 equal 100-cm^2 sections, to facilitate the sowing and subsequent locating and monitoring of seeds. On 9 June 1994, 25 *P. engelmannii* seeds were sown into the first 25 available sections. If rocks or surface roots prevented a seed from being sown in a particular section, we utilized an alternate section. Seeds received 160 ml of water upon sowing and an equal amount twice a week for 3 wk. Germination and survivorship were noted weekly until 9 October 1994 and again from 24 July to 23 September 1995. A chi-square analysis was used to test the null hypothesis that there were no differences in seed germination rates across the ecotone boundary.

Seedling survivorship was monitored using 3-yr-old nursery-grown *P. engelmannii* seedlings (Lawyer Nursery Inc.). On 9 June 1994 we planted seedlings every 0.25 m along the same 40-m rows unless obstructions such as rocks were present. Seedlings received 160 ml of water, approximately equal to 20 mm of precipitation, twice a week for 3 wk to facilitate establishment. Seedling survivorship was noted weekly until 9 October 1994 and on 16 July and 23 September 1995. A chi-square analysis was used to test the null hypothesis that there are no differences in seedling survival across the ecotone boundary.

Differences in seedling microclimates and potential causes of seedling mortality were assessed by logging weekly maximum and minimum temperatures 20 cm below the surface, at the soil surface, and 2 cm above the surface at the ecotone (0 m) and 30 m into both the forest and park in Willow Park from 9 June through 9 October 1994. Precipitation was also measured weekly at 30 m into the park during this period.

By germinating 72 *P. engelmannii* seeds and growing them in a greenhouse utilizing soils collected in Willow Park, we ascertained the influence of forest, ecotone, and park soils on root elongation and thus the potential for seedlings to reach subsurface moisture. Soils were collected to 30-cm depth at the ecotone (0 m) and 30 m into both the forest and park. The 2.5 × 20-cm tubes with seeds sown at 5-mm depth were watered daily. We harvested shoots and roots of 15-wk-old seedlings and, after measuring their lengths, dried them at 70°C. Root lengths and dry weight root:shoot ratios were analyzed using a one-way ANOVA.

Soil Analyses

Soil samples were obtained from a 2-cm-diameter core of soil extending from the surface to 30-cm depth along both transects in all 6 parks. The core excluded the O horizon. Soil-texture analysis was conducted for each core using the hydrometer method (Day 1965). Hydrometer readings were recorded at 0.5, 1, 2, 4, 8, 15, 30, 60, 120, 240, 480 min to construct soil particle-size distribution curves, and differences in percent sand, silt, and clay among locations along the transect were analyzed using a nested ANOVA (transects nested within parks).

Moisture available to plants in soil at field capacity was measured for 3 randomly selected soil samples collected at the ecotone (0 m) and 30 m into both the park and forest in Willow Park. Using a 1.5 MPa ceramic plate extractor (Soilmoisture Equipment Corporation), we measured soil water content at 0.010, 0.033, 0.5, and 1.5 MPa. Soil moisture available to plants was calculated utilizing the difference between water content at field capacity and at the permanent wilting point. These values are most closely correlated to water contents at 0.033 and 1.5 MPa, respectively (Peters 1965, Banister 1986). Differences in soil moisture available to plants among locations were analyzed using a one-way ANOVA.

RESULTS

Tree Morphology

Two of the 6 parks studied, Taylor Park and Union Park, were surrounded by seral *P. contorta* forest. Tree morphology along the *P. contorta* transects often exhibited exceptions to the consistent trends observed in the *P. engelmannii* forests surrounding the other 4 parks. Height:age, dbh:age, and height:dbh ratios, when all 6 parks were included, indicated significant interactions between parks and locations across the ecotone ($P = 0.005$, $P < 0.001$, and $P = 0.005$, respectively). Therefore, Taylor and Union Park data were excluded from further analyses and the consistent trends observed in the *P. engelmannii*–dominated ecotones are reported below.

P. engelmannii at the ecotone had a significantly higher height:age ratio ($P < 0.001$) and dbh:age ratio ($P < 0.001$), indicating more growth per year (Fig. 2). The height:dbh ratios showed that trees at the ecotone had grown more in girth than in height relative to trees in the forest interior ($P < 0.001$) (Fig. 2). Trees at the ecotone had a significantly lower coefficient of variation of tree-ring width ($P = 0.002$), indicating less year-to-year variation in growth increment (Fig. 2).

Seedling Establishment

At all 3 locations (forest, ecotone, and park) in Willow Park, no germination of sown seeds was noted in the 1994 growing season. Germination did occur in the 1995 growing season and was significantly higher in the forest (46%) than in the ecotone (28%) and park (5%; $P < 0.001$). Of the seeds that did germinate, total seedling survivorship at the end of the season (23 September 1995) was 18%, 32%, and 42% along the forest, ecotone, and park transects, respectively (Fig. 3). These seeds, tested in vitro in 1994, had a 93% germination rate.

Survivorship of planted 3-yr-old *P. engelmannii* seedlings was significantly higher in the forest (50%) and at the ecotone (52%) than in the park (8%) after 15 mon ($P < 0.001$; Fig. 4). While the primary cause of mortality appeared to be desiccation during the 1994 growing season, 73% of seedlings in the forest, 55% at the ecotone, and 0% in the park experienced herbivory. Removal of leader shoots during the winter accounted for most of the observed herbivory.

Seedling microclimate during the 1994 growing season was more severe in the park than the forest. Maximum and minimum soil temperatures at 20-cm depth were similar across the ecotone. However, at the soil surface and at 2 cm above the surface, seedlings in the park were consistently exposed to colder nights and warmer days compared to seedlings within the forest (Fig. 5). Precipitation exhibited a pattern typical of the Gunnison Basin, with a relatively dry June followed by

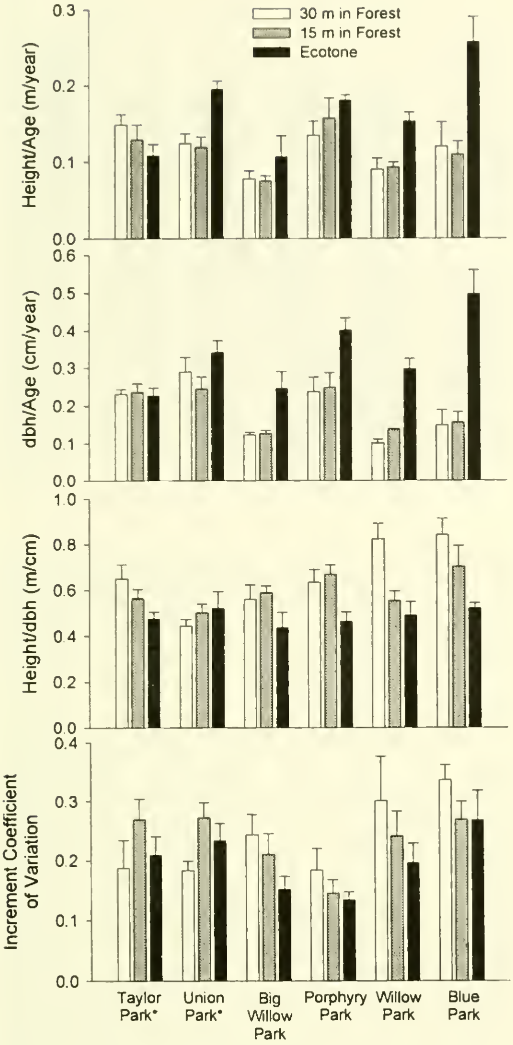

Fig. 2. Height:age ratio, dbh:age ratio, height:dbh ratio, and coefficient of variation of tree-ring width of trees near the forest-park ecotone in *Pinus contorta* (*)–dominated and *Picea engelmannii*–dominated treelines. Bars indicate standard errors ($n = 6$).

increased precipitation brought by afternoon thunderstorms in July and August.

P. engelmannii seedlings grown in forest, ecotone, and park soils showed no observable differences in growth. The mean root length of seedlings grown in forest (14.1 cm), ecotone (13.7 cm), and park (14.6 cm) soils did not differ significantly ($P = 0.534$). Dry weight root:shoot ratios of seedlings grown in forest, ecotone, and park soils were 0.67, 0.69, and 0.70, respectively, and did not differ significantly ($P = 0.764$).

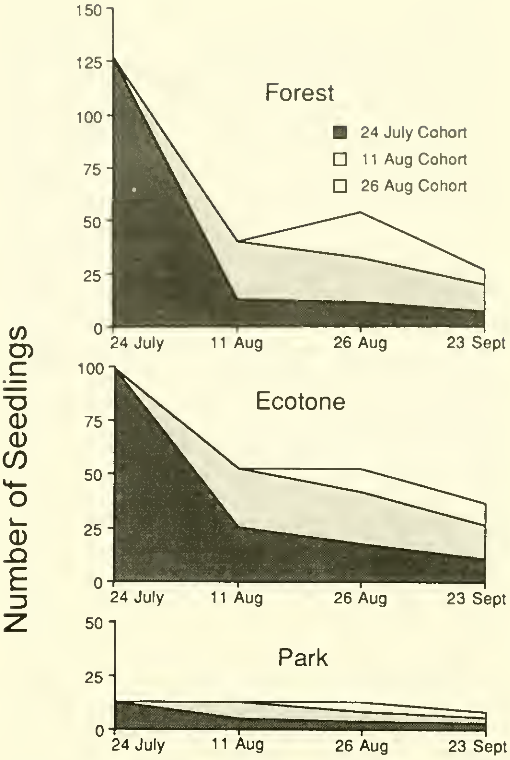

Fig. 3. Number of seeds germinated and survivorship of those seedlings in Willow Park. The 3 cohorts account for those seeds that germinated prior to 24 July 1995, between 24 July and 11 August 1995, and between 11 August and 26 August 1995.

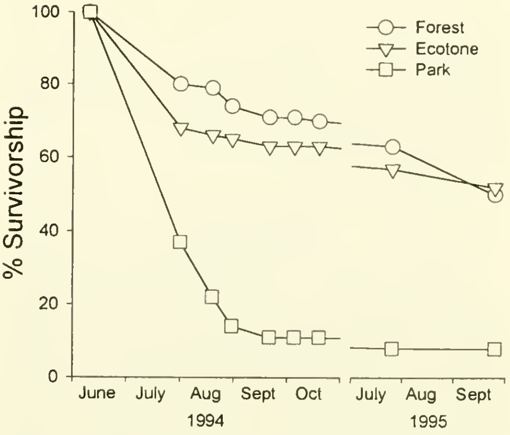

Fig. 4. Percent survival rate of 3-yr-old seedlings planted 9 June 1994 along a transect spanning the forest-park ecotone in Willow Park. Numbers of seedlings planted in the forest, ecotone, and park were 122, 145, and 160, respectively.

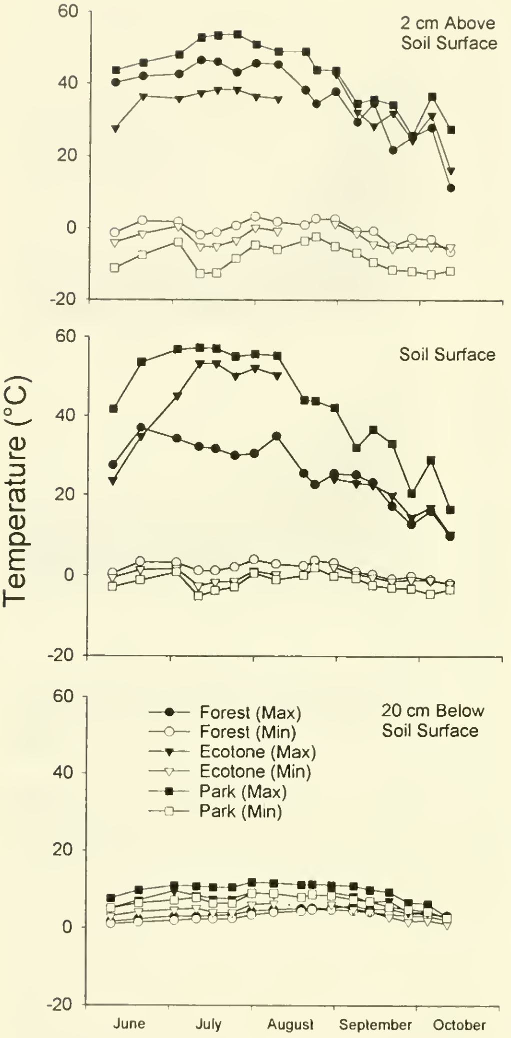

Fig. 5. Weekly maximum and minimum temperatures at 3 different locations within the seedling's microclimate along a transect spanning the forest-park ecotone in Willow Park. Temperature extremes were recorded weekly from 9 June through 9 October 1994.

Soil Analyses

While soils in all 6 parks were sandy loams, soil texture differed significantly ($P < 0.001$) across the forest-park ecotone. Forests had a mean of 8% more sand, 53% less silt, and 72% more clay compared with parks (Fig. 6). Moisture available to seedlings in soils at field capacity also differed significantly ($P = 0.011$) across the forest-park ecotone. There was 54% more water available to plants in forest soils at field capacity than in park soils at field capacity (Fig. 7).

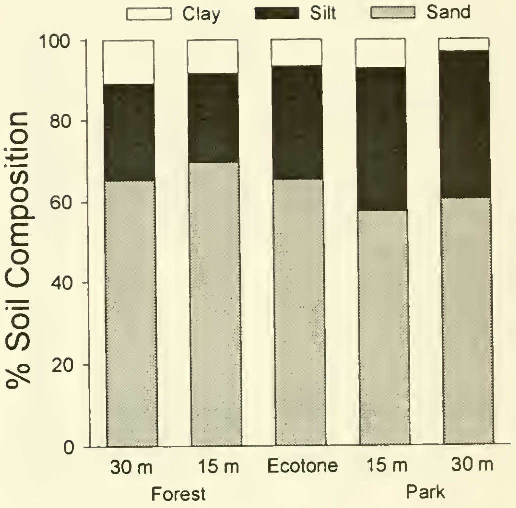

Fig. 6. Soil texture along transects spanning the forest-park ecotone. Percentages are the means of 6 parks with 2 transects per park and 3 replications per location ($n = 36$).

DISCUSSION

Tree morphology data indicated that stress of mature trees is an unlikely contributing factor to maintenance of forest-park ecotones in the Gunnison Basin. Trees at the ecotone appear no more stressed, possibly even more robust, than trees farther into the forest. The lower coefficient of variation of tree-ring width found in ecotone trees indicates less year-to-year variation in growth increment, suggesting a more uniform and less stressful environment (Fritts 1976). These results indicate that factors limiting seedling establishment contribute to the maintenance of parks in the Gunnison Basin, which corroborates the conclusion of Dunwiddie (1977) pertaining to meadows in Wyoming.

Seed germination and seedling survivorship of *P. engelmannii* were restricted in Willow Park, which further supports the contention that parks are maintained by limited establishment. The higher mortality of seedlings in the park may be due in part to the more extreme microclimate. Temperature extremes play an important role in the survival of *P. engelmannii* seedlings (Patten 1963, Kuramoto and Bliss 1970, Franklin et al. 1971, Root and Habeck 1972, Noble 1973, Moir and Huckaby 1994, Balisky and Burton 1995, Taylor 1995, Woodward et al. 1995), and the large diurnal fluctuations in surface and air temperatures

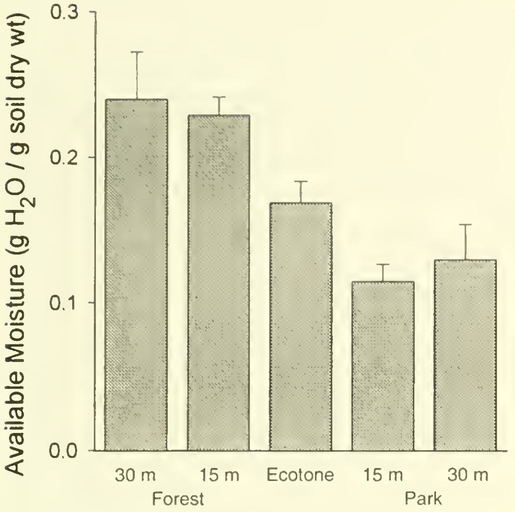

Fig. 7. Moisture available to plants in soil at field capacity for samples collected along the transect spanning the forest-park ecotone in Willow Park. Available moisture is the difference between water content at field capacity and water content at the wilting point. Bars indicate standard errors (n = 15).

common to meadows may inhibit tree invasion (Hellmers et al. 1970, Jakubos and Romme 1993). During the 1994 growing season, temperatures 2 cm above the soil surface in Willow Park fluctuated greatly, with a mean weekly maximum of 43°C and a mean weekly minimum of –8°C. Such temperature fluctuation alone may prove fatal to *P. engelmannii* seedlings. Hellmers et al. (1970) noted 0% survival of *P. engelmannii* seedlings grown in high day (35°C) and low night (3°C) temperatures. In addition, terminal bud formation was inhibited in high day temperatures of 35°C (Hellmers et al. 1970), which may increase mortality during the subsequent winter. Precipitation and temperatures for the 1994 and 1995 growing seasons were near normal at Lake City, Colorado, 36 aerial km west of Willow Park, indicating that weather data we recorded in 1994 were not unusual (United States Department of Commerce 1994, 1995).

Herbivory in parks could potentially limit establishment in subalpine meadows; however, herbivory alone does not appear to maintain the ecotone in Willow Park. Although seed herbivory by members of the seed bug family (Lygaeidae) was observed in 1994, preliminary observations of predation rates of seeds placed in wire-mesh containers at forest, ecotone, and park locations indicated that the potential for such herbivory was uniformly high (90–100%) across the ecotone. Removal of *P. engelmannii* cotyledons or terminal buds by herbivores may limit regeneration (Noble and Shepperd 1973, Noble and Alexander 1977), although the impact of shoot herbivory in Willow Park appears limited considering the observed damage of *P. engelmannii* seedlings was greatest in the forest where survivorship was highest. Cantor and Whitham (1989) suggest that aspen is excluded from meadows due to belowground herbivory by pocket gophers. Belowground herbivory by rodents, as indicated by soil mounds, accounted for a small portion of the *P. engelmannii* seedling mortality in Willow Park.

Variation in soil texture across the forest-park ecotones supports commonly cited suggestions that edaphic factors help maintain dry Rocky Mountain parks (Daubenmire 1943, Peet 1988, Knight 1994). Fine-textured soils in parks are more favorable for growth of sod-forming herbaceous vegetation, which may competitively exclude the establishment of tree seedlings (Stahelin 1943). However, if such competition were the primary factor maintaining parks, the treeline would be expected to advance into the park where shading from ecotone trees inhibits herbaceous vegetation (Daubenmire 1943). Park soils may increase tree seedling mortality by enhancing water stress. Fine-textured soils may slow water infiltration and thus increase drought severity (Knight 1994). Daubenmire (1943) suggested that inhibited root elongation in park soils increases susceptibility of tree seedlings to drought; this premise is not supported by our study where root growth was unaffected by soil texture. In Willow Park, park soils at field capacity do have less moisture available to plants, thus enhancing the potential for water stress, particularly in early summer when precipitation is minimal.

Factors limiting seedling survival can be further elucidated by observing the few locations where trees do establish in parks. Established trees in Willow Park are often well away from the ecotone and inevitably associated with willows (*Salix* spp.), which may be providing a mesic microclimate that facilitates tree establishment. Rochefort and Peterson (1996) found tree invasion in subalpine meadows in the Olympic Mountains to be associated with heath-shrub communities that may moderate soil temperature and moisture. On the other hand, the presence of willows may be indicative of moist soils that could promote seedling survival despite unfavorable soil texture.

Supporting the role of edaphic factors over climatic factors is the often prolific establishment of *P. engelmannii* and *P. contorta* observed in clear-cuts near the parks. Notable is Blue Park, where recent clear-cuts reached the forest-park ecotone. Here the ecotone appears to be maintained as *P. contorta* is regenerating only in previously forested areas. This indicates that while the climate is suitable for seedling establishment, it is the soil or the associated vegetation in parks that maintains forest-park ecotones in the Gunnison Basin.

ACKNOWLEDGMENTS

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COMPARISON OF THE EPIPROCT STRUCTURE OF TWO CLOSELY RELATED SPECIES, *SWELTSA FIDELIS* (BANKS) AND *S. REVELSTOKA* (JEWETT) (PLECOPTERA: CHLOROPERLIDAE)

Jennifer K. Delk[1], Mary Jane Kilgore[1], and Bill P. Stark[1,2]

ABSTRACT.—The male epiprocts of 2 closely related western Nearctic species, *Sweltsa fidelis* (Banks) and *S. revelstoka* (Jewett), were examined using SEM. The males of these 2 species have been historically distinguished by epiproct measurements. The ratio of the length from the base to greatest width versus total epiproct length ranges from 0.49 µm to 0.67 µm ($\bar{x}$ = 0.56) in *S. fidelis* and 0.55 µm to 0.69 µm ($\bar{x}$ = 0.60) in *S. revelstoka*. Similarities in measurement suggest that the location of the greatest epiproct width is not a reliable and consistent character for distinguishing males of these 2 species.

Key words: stonefly, Sweltsa, *epiproct, morphology, SEM, western North America.*

Sweltsa fidelis (Banks) and *S. revelstoka* (Jewett) are similar western Nearctic species with broadly overlapping geographical ranges in the northern Rocky Mountains and Cascades. Jewett (1955) noted that only a "slight difference" in lateral aspect of epiproct shape distinguishes males of the 2 species, although females are easily separated by subgenital plate shape (Surdick 1995). Jewett (1955) and Gaufin et al. (1972) suggested the *S. fidelis* epiproct was "about 1.7 times as broad near the tip as . . . near the base," whereas the epiproct of *S. revelstoka* was "less broad near the tip." Baumann et al. (1977) found the dorsal aspect of the epiproct tip of *S. fidelis* to be almost "twice as broad as base in dorsal view," and in *S. revelstoka* the tip was considered about the same width as the base. Surdick (1995) abandoned these characters in favor of the location of the greatest epiproct width as a means of separating males of these species, the greatest width occurring at 3/5 length in *S. fidelis* and at 3/4 length in *S. revelstoka*. This method also proved to be unreliable for distinguishing the males of these 2 species.

MATERIALS AND METHODS

Specimens examined are listed in Table 1. Each collection was identified to species by the examination of associated female specimens. Epiproct samples were taken by severing the last 4–5 abdominal segments from male specimens that had been stored in alcohol. Samples were placed in acetone and cleaned with an ultrasonic cleaner for 1 min. Samples were air-dried, placed on double-stick copper tape on SEM stubs, coated with gold palladium, and scanned using an AMRAY Model 1810 SEM. The length to the widest point and total length of the epiproct were measured using the "click and drag" function of the AMRAY computer control software. Results are presented in Table 2.

RESULTS AND DISCUSSION

Figures 1–4 indicate the close similarity in epiproct structure for *S. fidelis* and *S. revelstoka*. In dorsum, the *S. fidelis* epiproct (Fig. 1) appears wider than that of *S. revelstoka* (Fig. 3), but this difference is not supported by measurements. The range of widths present in *S. fidelis* specimens is 115–177µm ($\bar{x}$ = 147.6 µm), which is comparable to the spectrum of widths in *S. revelstoka*, 81.1–180 µm ($\bar{x}$ = 109.9 µm).

The ratio of the length from the base to the point of greatest width versus total length of epiproct ranges from 0.49 µm to 0.67 µm ($\bar{x}$ = 0.56) in *S. fidelis* and from 0.55 µm to 0.69 µm ($\bar{x}$ = 0.60) in *S. revelstoka*. Similarities in

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TABLE 1. Locality data for *Sweltsa fidelis* (Banks) and *S. revelstoka* (Jewett).

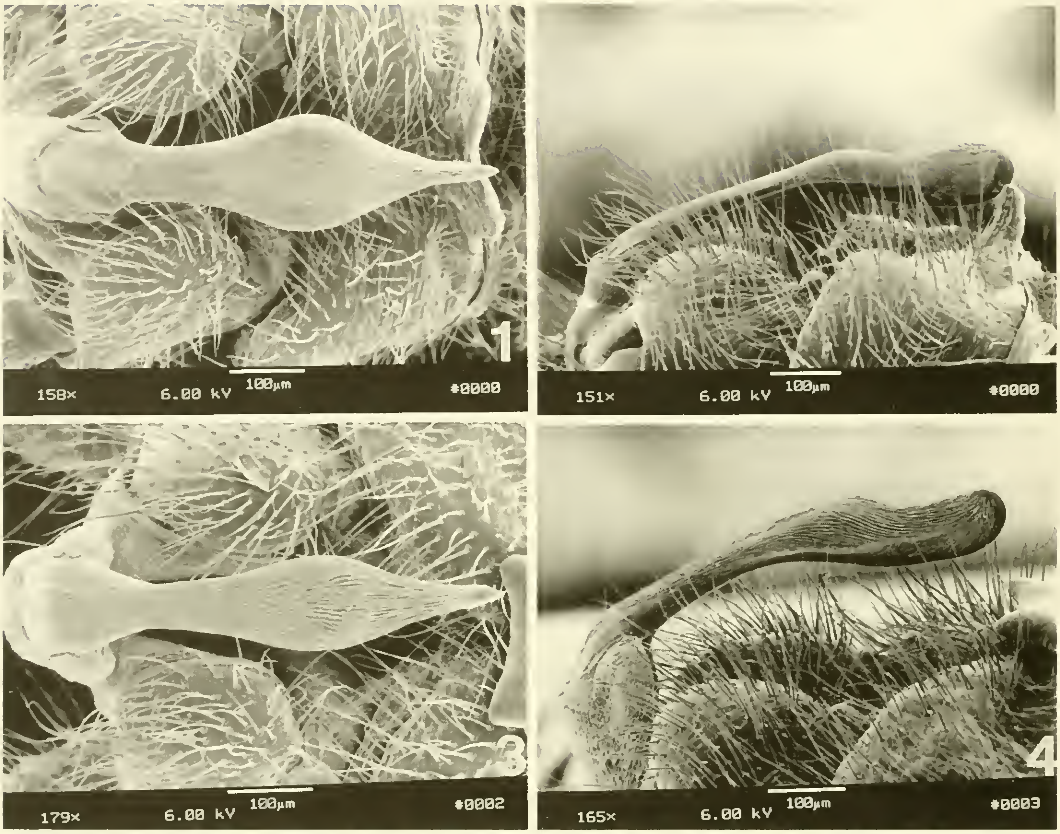
	Sweltsa fidelis		*Sweltsa revelstoka*
1A.	ID: Lemhi Co., Moose Creek blw Lost Trail Pass, 23-VII-1979, B. Stark, K. Stewart, R. Baumann, 5♂, 5♀	1B.	AB: Banff Nat. Pk., Moraine Creek, 27-VII-1972, A. Gaufin, 4♂, 3♀
2A.	MT: Gallatin Co., Hyalite Creek, Hyalite Squaw Creek Trailhead, 24-VII-1979, B. Stark, K. Stewart, R. Baumann, 1♂, 7♀	2B.	MT: Glacier Co., Iceberg Lake, Glacier Nat. Pk., 21-VII-1979, B. Stark, K. Stewart, R. Baumann, 1♂, 2♀
3A.	MT: Gallatin Co., Portal Creek, FS 984, 6 mi N Big Sky, 9-VI-1987, B. Kondratieff, 6♂, 1♀	3B.	OR: Clackamas Co., Still Creek Campground, Mt. Hood, 12-VII-1979, B. Stark, K. Stewart, 7♂, 3♀
4A.	MT: Glacier Co., Swift Current Creek near Red Rock Falls, 8-VII-1967, M. Miner, 4♂, 1♀	4B.	OR: Hood River Co., Salmon River tributary, Mt. Hood, 13-VII-1963, S. Jewett, 4♂, 2♀
5A.	MT: Granite Co., Butte Cabin Creek, 26-VII-1979, M. Miner, 44♂, 50♀	5B.	WA: Pierce Co., St. Andrews Creek, Mt. Rainier Nat. Pk., 13-VII-1979, B. Stark, K. Stewart, 16♂, 10♀
6A.	OR: Benton Co., Parker Creek, Mary's Peak Road, 26-VI-1985, B. Stark, 11♂, 16♀		
7A.	OR: Lane Co., 12.5 mi N Blue River, Andrews Exp. Forest, 6-VII-1978, B. Frost, 2♂, 2♀		
8A.	WA: Spokane Co., Deadman Creek, Mt. Spokane St. Pk., 11-VI-1991, B. Stark, R. Baumann, 7♂, 4♀		

TABLE 2. Epiproct measurements in µm for *Sweltsa fidelis* (Banks) and *S. revelstoka* (Jewett). LGW/TL = epiproct length to the point of greatest width divided by total epiproct length.

Site	# males	LGW/TL
S. fidelis		
1A	2	0.49–0.50
2A	1	0.57
3A	2	0.56
4A	1	0.52
5A	8	0.52–0.67
6A	1	0.56
7A	1	0.59
8A	2	0.58–0.60
		$\bar{x}$ = 0.56
S. revelstoka		
1B	2	0.57–0.60
2B	1	0.55
3B	2	0.60
4B	3	0.60–0.61
5B	8	0.56–0.69
		$\bar{x}$ = 0.60

measurements and the broad range present in both species suggest this character is not a consistently reliable means for distinguishing the 2 species.

Ricker (1939) and Frison (1942) record brachypterous males and females of *S. fidelis*, and Jewett (1955) describes both long-winged and brachypterous *S. revelstoka* adults. Surdick (1995) reports that *S. revelstoka* "commonly exhibits different degrees of brachyptery" while *S. fidelis* "is usually macropterous." In the present study all *S. fidelis* (*n* = 18) males were long winged, and 10 *S. revelstoka* males (*n* = 16) were brachypterous. These reported variations in wing length also bring into question the reliability of this character for distinguishing males of *S. fidelis* and *S. revelstoka*. No synonymy is suggested for these species at the present time because the female subgenital plates are so different, but distributional records based on isolated male specimens should be considered tentative until verified with female specimens.



Figs. 1–4. Scanning electron micrographs of *Sweltsa* epiprocts: 1, *S. fidelis*, dorsal aspect; 2, *S. fidelis*, lateral aspect; 3, *S. revelstoka*, dorsal aspect; 4, *S. revelstoka*, lateral aspect.

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STARVATION AND NESTLING EJECTION AS SOURCES OF MORTALITY IN PARASITIZED LAZULI BUNTING NESTS

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Key words: brood parasitism, nestling growth, Brown-headed cowbird, Molothrus ater, *host-parasite interaction.*

Many studies have documented a reduction in host nestling growth and the number of fledglings produced from nests of small hosts parasitized by Brown-headed Cowbirds (*Molothrus ater*; Nolan 1978, Scott 1979, Hatch 1983, reviewed in May and Robinson 1985, Marvil and Cruz 1989, Weatherhead 1989). A short incubation period (Nice 1953, Nolan 1978, Lowther 1993), loud begging calls (Friedmann 1929, Dearborn 1997), and larger relative mouth sizes (Ortega and Cruz 1991), coupled with a rapid growth rate (Norris 1947, Scott 1979, Hatch 1983, Lowther 1993), typically give the cowbird nestling a head start over host young. As a result, the larger cowbird nestling gapes higher than most host nestlings, which increases the probability of the cowbird being fed by host parents (Smith and Montgomerie 1991, Teather 1992, Leonard and Horn 1996). Thus, one potential cause of reduced reproductive success in parasitized nests of small host species could be a disproportionate provisioning of food to the young cowbird, resulting in starvation of host nestlings. However, I know of only a single study (Dearborn 1997) documenting the distribution of food among nestlings in parasitized nests.

In addition, several studies have implicated cowbird nestling ejection behavior as a source of host nestling mortality (Twomey 1945, Dearborn 1996). Cowbird nestlings ejecting host young have been video taped once (Dearborn 1996) and suggested by at least 2 other researchers (reviewed in Dearborn 1996). The extent to which this behavior occurs is not known, since most researchers assume missing host young are taken by predators or removed from the nest by parents after starving.

In this study I recorded feeding rates, size of food items delivered, distribution of food, and growth rates in parasitized and unparasitized nests of Lazuli Buntings (*Passerina amoena*). I specifically examined whether bunting nestlings in parasitized nests die due to starvation or to physical aggression from the cowbird nestling.

The primary study area is in western Montana in Missoula County on the western side of Mount Sentinel and Mount Jumbo. These mountains are part of the Sapphire Range and are located on the eastern edge of the city of Missoula. Elevations range from 1070 to 1719 m. Primary habitat is Palouse prairie, consisting of native bunchgrasses interspersed with shrubs.

From late May to August 1995, I monitored 2 parasitized and 16 unparasitized nests on Mount Jumbo and Mount Sentinel and weighed daily (to the nearest 0.1 g) cowbird and bunting chicks using a Pesola scale. I conducted 2-h behavioral observations of parasitized and unparasitized nests from a distance of 20–30 m using a variable-power spotting scope to record nestling behavior and the proportion of food delivered to cowbird and/or bunting nestlings. The size of food items delivered to each nestling was placed into 1 of 5 categories based upon the following criteria: 1 = hard to see, 2 = equal to bill length, 3 = just longer than bill, 4 = twice bill length, 5 = more than twice bill length. Volume of food per hour delivered to nestlings was calculated by multiplying the number of feeding trips per hour by average load size. Observation times were selected to ensure that parasitized and unparasitized nests were observed during the same times of day and under similar weather conditions.

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I used a Mann-Whitney U test (Zar 1996) to compare (1) day 3 weights of bunting nestlings in parasitized and unparasitized nests, (2) average nestling weights per nest on day 3 in parasitized and unparasitized nests, (3) volume of food per hour delivered to nestling cowbirds and buntings, and (4) average number of feeding trips per hour for parasitized and unparasitized nests. A binomial test was performed to compare the proportion of feeding trips in which only the cowbird was fed to the proportion of feeding trips in which just buntings were fed.

The day 3 weight of Lazuli Bunting nestlings in parasitized nests (n = 5 nestlings) was significantly lighter than the day 3 weight of Lazuli Bunting nestlings in unparasitized nests (n = 16 nestlings; Mann-Whitney U test, P = 0.0009). Recognizing that within-nest variation may confound this analysis, I then averaged the day 3 weights for each nest. The average day 3 weight of Lazuli Bunting nestlings differed between parasitized and unparasitized nests ($\bar{x}$ = 1.84 g ± 1.15 s and 4.28 g ± 0.349, respectively; Mann-Whitney U test, $P < 0.10$). Small sample size prevents significance; however, each of the 3-d-old bunting nestlings in parasitized nests weighed less than the lightest 3-d-old bunting nestlings in unparasitized nests. By day 4 all 5 bunting nestlings in parasitized nests were dead. A graph of nestling mass over time shows a steady decline in weight of host nestlings in parasitized nests (Greene et al. 1996).

I observed 57 feeding trips at 2 parasitized nests. In the 1st nest, the cowbird hatched the same day as 1 bunting nestling and the day before the other bunting nestling. In the 2nd nest, the cowbird nestling hatched 1 d before 3 bunting nestlings. All observed feeding trips occurred 1–3 d after hatching. Of 57 feeding trips observed at 2 parasitized nests, 32 of 46 resulted in only the cowbird being fed at 1 nest (binomial test, P = 0.02), and 11 of 11 resulted in only the cowbird being fed at the 2nd nest (binomial test, $P < 0.001$).

I observed an average of 6.75 (s = .992) feeding trips per hour for 6 unparasitized nests (n = 87 feeding trips to 18 nestlings) where bunting nestlings were 1–3 d old. This did not differ significantly from the average 6.14 (s = 1.86) feeding trips per hour in 2 parasitized nests (n = 36 feeding trips to 5 nestlings) where bunting nestlings were 1–3 d old (Mann-Whitney U test, P = 0.39). These results should be interpreted with caution since the power of this test is low. There was a trend toward cowbird nestlings (18.46 per hour) receiving a larger volume of food per hour than bunting nestlings (11.64 per hour; Mann-Whitney U test, P = 0.06).

The relative strength of the provisioning stimulus provided by bunting nestlings did differ between parasitized and unparasitized nests. Lazuli Bunting eggs in the same nest usually hatch on the same day (Greene et al. 1996). Consequently, the degree of development and corresponding height of the gape of bunting nestlings between 1 and 4 d of age in unparasitized nests were relatively even. However, I observed that at every feeding trip to parasitized nests, the gape of the cowbird nestling was at least 2.5 cm higher than the gape of the bunting nestlings. For all 36 observed feeding trips to parasitized nests during days 1 and 2, at least 1 bunting nestling could be seen begging. But after day 2 of receiving less than 20% of the food delivered to the nest, the bunting nestlings in parasitized nests often did not gape when an adult arrived with food. By day 4, both bunting nestlings in 1 parasitized nest died of starvation and were found flattened in the bottom of the nest. Two bunting nestlings in the 2nd parasitized nest also died of starvation on day 4. The third 4-d-old bunting nestling was found dead on the ground below the 2nd parasitized nest.

My observations reveal that gaping and jostling for position by the much larger cowbird nestling often move the bunting nestlings around inside the nest. Most of these interactions appear to be nonaggressive; however, on 2 occasions I witnessed what appeared to be aggressive head pecking by cowbird nestlings. On 4 separate occasions I witnessed a single 3-d-old bunting nestling settle onto the back of a 4-d-old cowbird nestling. In every instance, the cowbird raised up on its legs within 1–3 sec and moved backwards or to the side for 3–12 sec until the bunting nestling was no longer touching its back. On 2 occasions this resulted in the 3-d-old bunting nestling lying on its side perpendicular to the rim of the nest with its head outside the nest and the rest of its body directly on the rim. In both instances the bunting nestlings raised their heads and fell back into the nest within 3–5 sec. Upon returning to this nest the next day, I found 2 bunting nestlings dead inside the nest and the 3rd bunting nestling lying on the ground directly below the nest.

In addition to mortality from inclement weather, nestling predation, physical aggression from cowbird chicks, and ectoparasites, my results suggest that another cause of reduced nestling survival in parasitized Lazuli Bunting nests is starvation, which results from cowbird nestlings receiving most of the food delivered to parasitized nests. While this appears to be the primary factor responsible for reduced reproductive success in parasitized Lazuli Bunting nests, my observations of nestling activity also reveal that host young may be indirectly ejected from the nest as the cowbird nestling attempts to maintain its position.

The relative importance of ejection as a source of mortality and the ability of cowbirds to eject host species larger than Indigo or Lazuli Buntings remains unknown (Dearborn 1996). Given that nestlings of many small host starve in parasitized nests (Mayfield 1977, Payne 1977, Nolan 1978, Marvil and Cruz 1989), ejecting them would seem to do little to increase cowbird nestling fitness. However, many host species nestlings gain weight normally (Field sparrow [*Spizella pusila*], Carey et al. 1994; Common Grackle [*Quiscalus quiscula*], Peer and Bollinger 1997; Prothonotary Warbler [*Protonotari citrea]*, Petit 1991; Red-winged Blackbird [*Agelaius phoeniceus*] and Yellow Warbler [*Dendroica petechia*], Weatherhead 1989; Dickcissel [*Spiza americana*], Hatch 1983) in parasitized nests, and ejecting them would likely increase the fitness of cowbird nestlings.

Another possible factor influencing ejection of host young could be nest shape. Nest shape varies both within and among species. Twenty-six Lazuli Bunting nests from my study site varied in depth from 3 to 5.5 cm, averaging 3.5 cm (Greene et al. 1996). A nest depth of 3–4 cm is typical of many cowbird host species; however, there is considerable variation in nest depth of cowbird hosts (Harrison 1975). Species with shallow nest cups may lose proportionally more young due to ejection than species with deep nest cups. Given the recent evidence in support of cowbird nestling ejection behavior, I would encourage researchers to consider this behavior and its potential impacts on cowbird fitness in future studies of nest parasitism.

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OBSERVATIONS OF BLACK-BILLED MAGPIES (*PICA PICA*) GROOMING FERAL HORSES (*EQUUS CABALLUS*)

Michael C. Ashley[1]

Key words: Black-billed Magpies, Pica pica, *feral horses, grooming habits.*

On 4 March 1995 I was observing feral horses (*Equus caballus*) in the southeast section of the Granite Range in Nevada (latitude 40°47′19″ North, longitude 119°18′13″ West) (Fig. 1), when I witnessed an interaction between a Black-Billed Magpie (*Pica pica*) and 2 of my study animals. The magpie alighted on the back of the 1st horse and moved around the animal's back. The magpie appeared to be scanning each new section of the horse's back as it moved, occasionally making pecking movements with its head, presumably removing ectoparasites from the animal. After about 3 min, the magpie left the 1st horse and landed on the back of the 2nd animal. It repeated its searching and picking behavior, this time moving onto the horse's neck and searching extensively through its mane. After 5 min on the 2nd horse, the magpie returned to the 1st and searched its mane for more than 1 min. Neither horse attempted to displace the magpie and both remained quiet throughout the visitations, suggesting familiarity with this behavior. I was able to closely observe the magpie behavior with a Kawa 22–60X spotting scope from ~20 m.

On 17 February 1996 I saw a repeat of this behavior with 2 magpies and 2 different feral horses. This episode occurred approximately 2 km east-southeast of the 1st observation but within the same valley. A magpie landed on top of the withers of the 1st horse and moved about its back for 3 min, occasionally picking at the horse's back.

During the same period a 2nd magpie flew to a nearby sagebrush (*Artemisia tridentata*) and appeared to be watching the behavior of the 1st bird. The 2nd magpie then flew to the back of a 2nd horse and proceeded to search and pick for approximately 3 min. During the grooming bout this magpie climbed into the mane of the horse, again without any adverse response. The wind was variable, 10–15 kph, and stronger gusts occasionally caused the 2nd magpie to struggle to maintain its footing. In one instance the horse twitched, dislodging the magpie.

I next observed 2 magpies grooming a yearling feral horse on 12 April 1997 in the Granite Basin, approximately 7 km south-southwest of the previous 2 sightings. This encounter lasted slightly more than 10 min. One of the magpies groomed the horse's rump, back, and dorsal area of its neck up to the base of its skull. The 2nd magpie clung to and groomed the ventral surface of the animal's neck for more than 1 min, moved to the inner aspect of the right foreleg at the hock for 4 min, and then briefly returned to grooming the underside of the horse's neck. Although there were periods when one or the other of the birds was not on the horse, there were 2 magpies grooming the animal simultaneously for more than 5 min.

The regularity and extent of this behavior is impossible to determine at this time. In more than 50 trips to this area, I have witnessed only these 3 incidents involving magpies and feral horses. The distances between observations at the Granite Ranch site and between Granite Ranch and Granite Basin can lead one to believe that magpies in this area search for horses to groom rather than wait at an established feeding station as described by Isenhart and DeSante (1985) for Scrub Jays (*Aphelocoma coerulescens*) cleaning Columbian black-tailed deer (*Odocoileus hemionus columbianus*). That conclusion, however, cannot be supported

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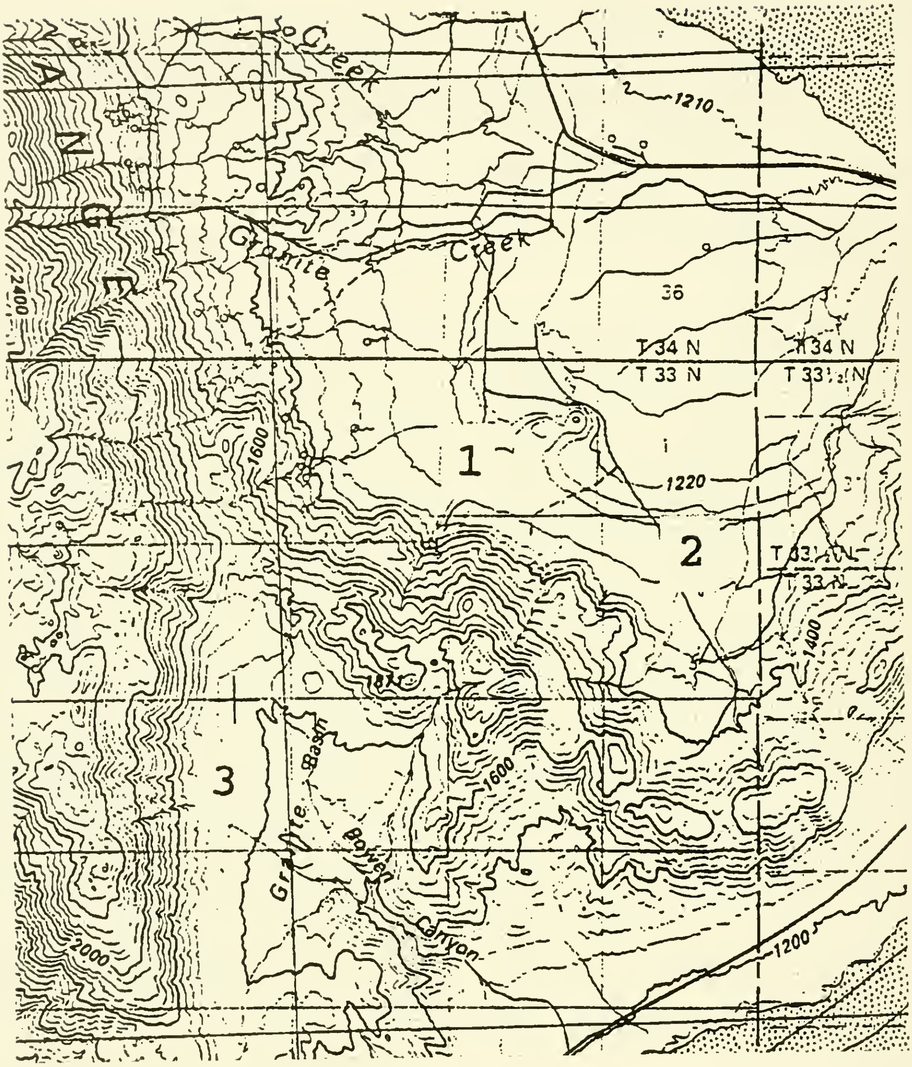

Fig. 1. Locations of grooming events: (1) Granite Ranch, 4 March 1995; (2) Granite Ranch, 17 February 1996; (3) Granite Basin, 12 April 1997. Enlarged from U.S. Geological Survey 1:100,000 Gerlach, NV, map.

by the small number of observations and lack of individual identification of the birds involved. On 3 occasions I have seen magpies in the vicinity of feral horses in even more remote sites in the Granite Range; however, I saw no grooming.

Magpies exhibit a variety of opportunistic foraging practices including scavenging, preying on nests (Groom 1993, Pampush and Anthony 1993), preying on small mammals (Goulden 1975), and grooming large herbivores (Dixon 1944, Linsdale 1946, Linsdale and Tomich 1953, Massei and Genov 1995). Magpies are reputed to probe sores on the backs of domestic and wild animals that are in poor physical condition (Bendire 1895). All of the horses I observed being groomed by magpies were in excellent condition. Because I viewed the behaviors closely, from <20 m with a 22–60X spotting scope, I am confident that grooming took place. I suspect the magpies were removing ectoparasites from the animals, not probing sores. Ticks (Parasitiformes: Metastigmata) are abundant mammalian ectoparasites in the Granite Range and are likely objects of the magpies' behaviors.

These observations add to the number of apparently mutualistic interactions between corvids and large herbivores. This extensive relationship includes (1) Black-billed Magpies (Linsdale 1946), Yellow-billed Magpies (*Pica nuttali*) (Linsdale and Tomich 1953), and California Scrub Jays (*Aphelocoma californica*) (Dixon 1944) interacting with mule deer (*Odocoileus hemionus*); (2) Black-billed Magpies (Linsdale 1946) with elk (*Cervus canadensis*); (3) Florida Scrub Jays (*Aphelocoma coerulescens*) with white-tailed deer (*Odocoileus virginianus*) (Fitzpatrick and Woolfenden 1996); (4) Scrub Jays (*Aphelocoma coerulescens*) with Columbian black-tailed deer (*Odocoileus hemionus columbianus*) (Isenhart and DeSante 1985); (5) Common Crows (*Corvus brachyrhynchos*) with cattle (*Bos taurus*) (Kilham 1982); and (6) Common Crows (*Corvus brachyrhynchos*) (Kilham 1982), Florida Scrub Jays (*Aphelocoma coerulescens*) (Baber and Morris 1980), Black-billed Magpies, and Carrion Crows (*Corvus corone cornix*) with feral hogs (*Sus scrofa*) (Massei and Genov 1995).

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FISH PREDATION ON GIANT WATER BUG (HETEROPTERA: BELOSTOMATIDAE) EGGS IN AN ARIZONA STREAM

Robert L. Smith[1] and Chris Horton[2]

Key words: Abedus herberti, *brooding, egg predation, aquatic insect, fish diet, stomach contents.*

We caught 3 brown trout (*Salmo trutta*) in the White Mountains of east central Arizona just after daybreak on the morning of 20 April 1997. The fish were taken in the South Fork of the Little Colorado River, elevation ca 2350 m, ca 10 km southeast of Springerville, Arizona. The 3 fish ranged in size from 18 to 20 cm TL. The brown or German trout, a European species, has been widely distributed in the United States since its introduction to North America in the late 19th century (Carlander 1969). This species was introduced to the White Mountains of Arizona sometime in the 1920s (Miller 1972). Brown trout are produced in hatcheries and released in Arizona streams including the Little Colorado River to provide a sports fishery.

Pooled stomach contents of the 3 fish contained 27 Trichoptera (Helicopsychidae and Limnephilidae) larvae in their cases, 5 mayfly nymphs (Baetidae), 3 Plecoptera (nymphs and adults), 2 aquatic Heteroptera (a naucorid and an early instar belostomatid), plus a variety of terrestrial insects. In addition to these items, one of the trout stomachs contained 10 giant water bug (*Abedus herberti* Hidalgo) eggs. The eggs, white in color with tan apices, were in good condition and contained mucilage on their distal ends. From this evidence we infer that the ova had recently been laid and, soon after their deposition, consumed by the fish. Brown trout are able to feed at starlight (10^{-4} foot Lamberts) intensities (Robinson 1978); thus, the eggs were probably eaten during the night.

Giant water bugs, aquatic Heteroptera in the family Belostomatidae, are found in tropical and temperate freshwater habitats throughout most of the world. In members of the giant water bug subfamily Belostomatinae, females glue their eggs to the backs of their mates, and the males then actively brood the eggs in a variety of ways (Smith 1997). Most belostomatines inhabit lentic habitats, but species in the New World genus *Abedus* are stream dwellers (Menke 1960). *Abedus herberti* occurs in Arizona streams at elevations of ca 1000–3000 m. Males of this species brood their eggs by exposing them to the atmosphere while resting on vegetation or rocks such that the bug is submersed with the tops of the eggs exposed to the air. When below the surface of the water, encumbered *A. herberti* males aerate their eggs by "brood-pumping," i.e., rocking longitudinally about once per second to circulate water over the eggs for embryonic respiration (Smith 1976).

When *Abedus* spp. eggs are first laid, they are white in color with tan caps. As the eggs develop, they take on a grayish color and enlarge. Near hatching time the dorsal portion of the chorion becomes ash gray. In all stages of development, eggs are highly conspicuous against the male's dark brown back. Giant water bug ova are among the largest insect eggs. Fully developed *Abedus herberti* eggs can reach 6 mm in length and 2 mm in width. Adult *Abedus herberti* bugs range from 24.5 to 40 mm in length and 12.5 to 22 mm wide (Menke 1960). Thus, the size of adult bugs substantially exceeded the gape of the small trout we caught.

Prior to this observation there have been no reports of predation or parasitism of any kind on giant water bug eggs, nor have these huge insect eggs ever been noted in the stomach contents of fish. It seems possible that fisheries biologists who routinely sample sports fish stomach contents might not have recognized giant water bug eggs for what they are.

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However, it is not surprising that these conspicuous eggs attached to actively brooding giant water bugs would attract the interest of foraging fish who might regularly snatch eggs from encumbered male bugs' backs. If this is the case, fish could be significant predators of *Abedus* spp. eggs throughout the range of the genus from southern Utah through Arizona and Mexico to Central America. It is also possible that the eggs were inadvertently ingested when the small fish attempted to eat a very large bug. The authors would be grateful for any additional accounts of giant water bug eggs found in fish stomachs.

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ALGAL COMPOSITION OF MICROBIOTIC CRUSTS FROM THE CENTRAL DESERT OF BAJA CALIFORNIA, MEXICO

Valerie R. Flechtner[1], Jeffrey R. Johansen[1], and William H. Clark[2]

ABSTRACT.—A total of 66 algal species representing 32 genera were recovered from soils of 10 sites in the Cataviña region of the Central Desert of Baja California, Mexico. The most common species encountered were the cyanophytes *Nostoc commune* and *Schizothrix calcicola*, the chlorophyte *Myrmecia astigmatica*, and the diatoms *Hantzschia amphioxys*, *Hantzschia amphyoxys* f. *capitata*, *Luticola cohnii*, *Luticola mutica*, and *Pinnularia borealis* var. *scalaris*. Nine species not found in any previous studies of North American desert soils were present in our study sites, including 3 taxa new to science: *Cylindrocystis brebissonii* var. *deserti*, var. nov.; *Elakatothrix obtusata*, sp. nov.; and *Fasciculochloris mexicana*, sp. nov. Attempts to correlate species composition with soil chemical and physical parameters were unsuccessful apart from a pH effect on cyanobacterial distribution. Overall composition of the soil algal community in the Cataviña region is distinct from other desert sites we have studied, although some cosmopolitan desert soil taxa were present.

Key words: algae, soil; Mexico, Baja California; Central Desert; Cataviña; cryptogamic crusts; Cylindrocystis brebissonii *var.* deserti; Elakatothrix obtusata; Fasciculochloris mexicana; *microbiotic crusts.*

Microbiotic crusts, also called cryptogamic crusts, cryptobiotic crusts, and microphytic crusts, are common in many arid and semiarid areas in the western United States (St. Clair and Johansen 1993). They consist of lichens, mosses, algae, and fungi, which form water-stable surface aggregates that have been demonstrated in some regions to be important in stabilizing soil and preventing erosion (Harper and Marble 1990, Johansen 1993, Williams et al. 1995, Williams, Dobrowolski, and West 1995). Furthermore, many of the free-living and lichenized cyanobacteria fix atmospheric nitrogen and can be significant contributors to desert nitrogen budgets (Rychert and Skujins 1974, Evans and Ehleringer 1993, Belnap 1996). Crusts are susceptible to damage by livestock, backpackers, and off-road vehicular traffic, which disrupt the crust, compact the soil, and if frequent enough, kill algal, lichen, and moss components of the crust (Kleiner and Harper 1972, Anderson et al. 1982). Rangefire can also seriously impact the crust community (Johansen et al. 1982, 1984, 1993). Natural

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recovery from disturbance can take from a few to many years (Anderson et al. 1982, Johansen et al. 1984, 1993, Callison et al. 1985).

Interest in the algal component of these communities has increased in recent years. Early investigators of these algae were intrigued by the occurrence of a group of organisms generally thought to be aquatic in such an extremely arid environment. Floristic work has demonstrated the presence of a number of algal genera, some of which also occur in aquatic habitats, and many of which are confined to terrestrial ecosystems. Most freshwater divisions are represented: Cyanophyta, Chlorophyta, Eustigmatophyta, Chrysophyta, Xanthophyta, Bacillariophyta, and Euglenophyta. In previously published work researchers tended to focus on 1 or 2 taxonomic divisions. The cyanobacteria are probably the best studied group because identifications can be made based on morphotypes in moistened soils, although there is considerable disparity between cyanobacterial floras based on mixed cultures and those based on unialgal isolates. Diatoms are usually superficially treated, although Rushforth and researchers trained in his laboratory have found considerable diversity in this group by direct preparation of soil diatoms (Anderson and Rushforth 1976, Johansen et al. 1981, 1984, Ashley et al. 1985, Johansen and St. Clair 1986). Green algae, although abundant and ubiquitous, are much less thoroughly studied due to the necessity of working with unialgal isolates in which details of life history (i.e., zoospore morphology, color changes with senescence, etc.) are required for correct placement in genus and species. Johansen et al. (1993) made some effort to identify green algal isolates and demonstrated the potential diversity of coccoid chlorophytes in soils.

Most recent papers dealing with taxonomy and distribution of desert soil algae study the semiarid shrub steppe and cool deserts in the Great Basin and Colorado Plateau provinces (see Johansen 1993 for a review of these papers). Most work on soil algae of hot deserts was done in the early 1960s. These studies include both the Sonoran (Cameron 1960, 1964, etc.) and Mojave (Durrell 1962, Shields and Drouet 1962, Hunt and Durrell 1966) deserts. To our knowledge, the Chihuahuan Desert soil algal flora has not been studied, although a single report of soil algal density does exist (Cameron 1969). All work on hot deserts emphasizes the cyanobacterial component of the soil community.

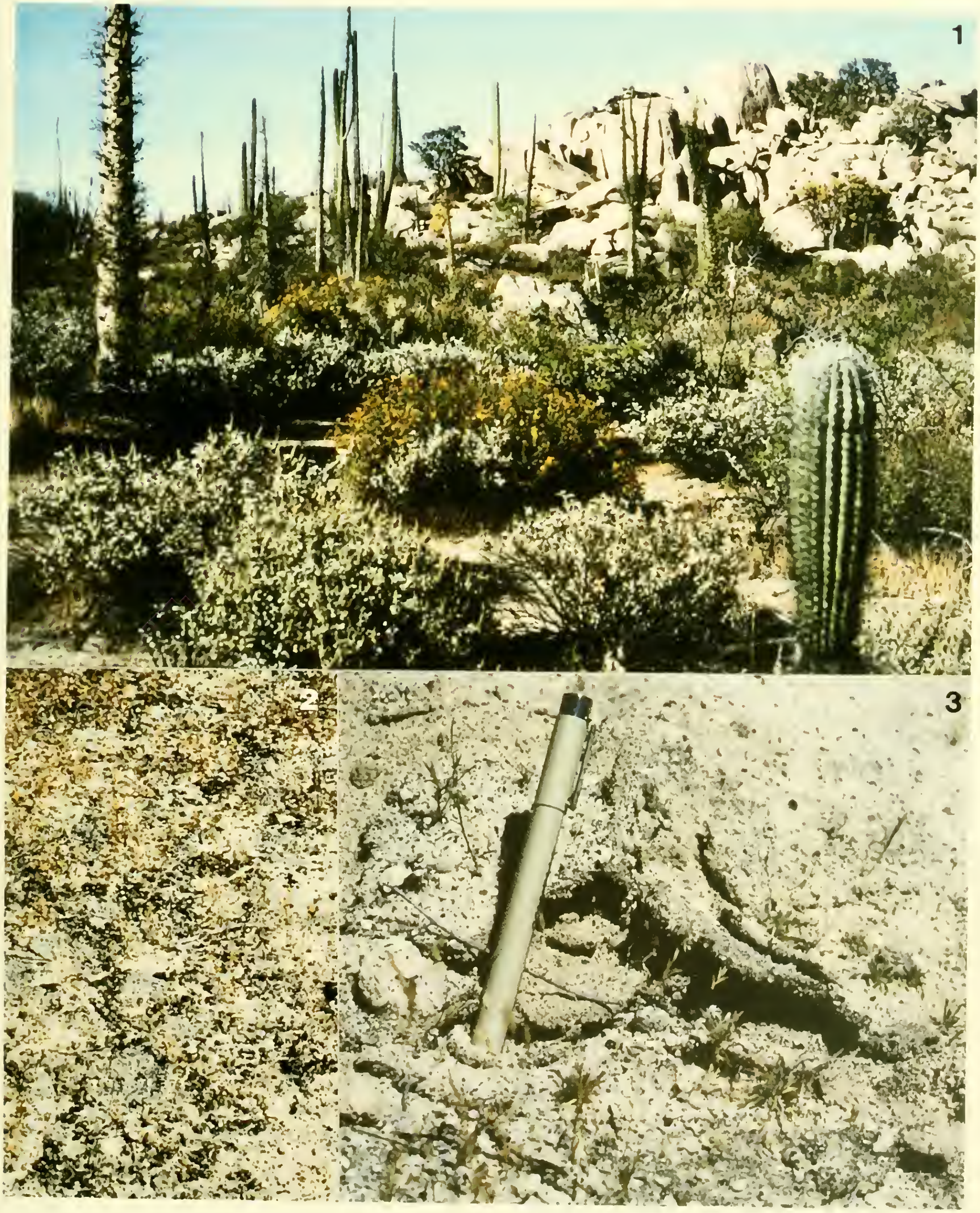
The objectives of the present study were twofold. First, we wished to carefully characterize the algal community from the Central Desert of Baja California, Mexico, a hot desert region previously unstudied with regard to its soil algal flora. Second, we wished to test for correlations between algal composition and soil chemical and physical properties in sites with highly similar climate. Although soil chemistry has been considered important in determining soil algal distribution (Starks et al. 1981), correlations between taxa in desert soils and soil chemistry have not been made.

MATERIALS AND METHODS

Study Area

Ten study sites were established in the Cataviña area of the Central Desert of Baja California, Mexico (Fig. 1), a mid-peninsular location 9 km northwest of Rancho Santa Ines (28°46′N, 114°46′W, 550 m elevation). The geology is dominated by weathered Cretaceous granite (tonalite) of the Jaraguay block (Grastil et al. 1975), the decomposition of which forms a coarse, sandy-textured soil (Blom and Clark 1984). Mean annual precipitation has been reported to range from 46 mm (Blom and Clark 1984) to 101.7 mm (García 1981). Mean annual temperature is 18–19°C, with a summer mean of 25.8°C, a winter mean of 13.2°C (Hastings 1964, Hastings and Humphrey 1969, García 1981), and occasional freezing temperatures. The vascular plant community is dominated by *Larrea tridentata* (Sesse and Moc.) Coville and *Ambrosia chenopodifolia* (Benth.) Payne, with species of *Opuntia* being the most common cacti. At each of the 10 sites, we recorded presence of all perennial vascular plant species adjacent to the collection site (Table 1). Microbiotic crusts formed significant cover in intershrub/intercacti spaces (Figs. 2, 3). The 10 sites will be referred to as Sites 1–10 in this paper. They correspond to W.H. Clark field collection numbers 9573–9582. Specific locations for each sample site are as follows:

Site 1, 29°47′04.2″N, 114°46′11.1″W;
Site 2, 29°46′57.3″N, 114°46′12.4″W;
Site 3, 29°47′07.8″N, 114°46′04.9″W;
Site 4, 29°47′10.5″N, 114°46′10.5″W;
Site 5, 29°47′17.7″N, 114°46′16.2″W;



Figs. 1–3. Cataviña area in Baja California, Mexico: 1, general topography and vegetation; 2, microbiotic crust at Site 10; 3, detail of algal crust, raised by slight disturbance (scale = 12 cm).

Site 6, 29°47′08.7″N, 114°46′29.2″W;
Site 7, 29°47′09.0″N, 114°46′27.9″W;
Site 8, 29°46′44.4″N, 114°46′03.9″W;
Site 9, 29°46′47.8″N, 114°46′04.8″W;
Site 10, 29°47′03.9″N, 114°46′08.4″W.

Sample Collection

Sample areas, all within a 2-km area, were chosen to represent various soil types and habitats present. We obtained the precise location of each site with a Sony PYXIS IPS-760 global

TABLE 1. Perennial vascular plant species present in each of the 10 Cataviña sites.

Species	Sites									
	1	2	3	4	5	6	7	8	9	10
Ambrosia chenopodifolia (Benth.) Payne		X	X	X				X	X	X
Ambrosia dumosa (Gray) Payne	X			X	X					
Atriplex polycarpa (Torr.) S. Wats.						X				
Ceratoides lanata (Pursh) Howell					X					
Encelia californica Nutt.						X	X		X	
Eriogonum fasiculatum Benth.								X		
Larrea tridentata (DC.) Cov.	X	X	X	X	X			X		
Lycium californicum Nutt. ex Gray					X	X				
Opuntia cholla Weber									X	
Opuntia ganderi (Wolf) Rebman & Pinkava							X	X		
Opuntia molesta Brandegee									X	
Prosopis glandulosa var. *torreyana* (L. Benson) Johnston							X			
Simmondsia chinensis (Link) Schneider					X					
Solanum hindsianum Benth.								X		
Viguiera laciniata A. Gray		X				X		X	X	
Viscainoa geniculata (Kell.) Greene						X	X			

positioning system. Vascular plant cover and percent visible coverage by microbiotic crust were noted for each plot and recorded photographically. Composite crust samples consisting of 10 cores (top 3 cm) were taken in a 2 × 2-m area at each site. Additional samples for soil chemistry analysis were collected from the center of each plot. Samples were dry when collected (29–30 April 1995), and we transported them to the laboratory within 1 wk of collection, where they were stored under refrigeration until analysis.

Characterization of Non-diatom Algae

Composite samples were crushed and mixed to produce a homogenous sample. A 1-g aliquot was removed and added to 99 ml of a 0.7% saline solution (as an osmotic protectant) for a 10^2 dilution of the original sample. Aliquots of 0.1 or 0.2 ml were spread in triplicate on agar solidified Z-8 medium (Carmichael 1986) for quantitation of Cyanophyta and on Bold's basal medium (BBM, Bold and Wynne 1978) for quantitation of non-diatom eukaryotic algae. Cultures were allowed to dry overnight before inversion, sealed with parafilm, and incubated in constant light at 20–23°C until good growth had been obtained (3–6 wk). We then counted the number of colony-forming units on each plate. For identification of Cyanophyta, wet mounts prepared directly from individual isolates on Z-8 plates were examined using an Olympus BH-2 photomicroscope with Nomarski DIC optics and photographed using Kodak PKL-135 film. Identification was made on the basis of cell and colony morphology using standard authoritative references (Geitler 1930–32, Desikachary 1959, Kantz and Bold 1969). For identification of non-diatom eukaryotic algae, individual isolates were picked into 5 ml liquid BBM and incubated 2–4 wk until good growth had been obtained. Identification was made on the basis of life history and morphological criteria using standard authoritative references (Komárek and Fott 1983, Ettl and Gärtner 1995). Because many cyanophytes grow poorly on artificial media, additional identification of cyanophytes was made directly from wet mounts of wetted soil samples incubated 48–72 h in the light.

We prepared type materials in 2 ways. Holotype material was prepared by filtering a young, healthy culture onto glass fiber filters that had been ashed and subsequently handled with forceps to minimize the possibility of eukaryotic DNA contamination. The filters were allowed to air dry, placed in glassine envelopes attached to herbarium cardstock, and then wrapped in herbarium envelopes. These materials were then deposited in the Herbarium of Nonvascular Cryptogams at the Monte L. Bean Museum, Brigham Young University, Provo, Utah. Unialgal cultures having isotype or paratype status were grown on agar slants of BBM and deposited in the UTEX Culture Collection at the University of Texas, Austin, Texas.

TABLE 2. Summary of species abundance and richness data for each of the 10 study sites in the Cataviña region of the Central Desert of Baja California, Mexico. Abbreviations used: CFU/g = colony-forming units of algae/gram soil, CYANOB = number of cyanobacterial taxa, EUKARY = number of non-diatom eukaryotic taxa, DIATOM = number of diatom taxa, TOTAL = total number of algal taxa, VASCUL = number of perennial vascular plant taxa, % CRUST = estimated percent cover of microbiotic crust.

Site	CFU/g	CYANOB	EUKARY	DIATOM	TOTAL	VASCUL	% CRUST
1	2×10^4	4	6	6	16	2	100
2	6×10^3	2	4	6	12	2	90
3	2×10^4	7	8	6	21	2	80
4	2×10^4	9	11	6	26	3	ND
5	8×10^3	7	4	8	19	4	55
6	5×10^4	6	6	6	18	6	100
7	5×10^4	6	10	8	24	5	100
8	2×10^4	6	8	7	21	5	100
9	1×10^4	4	14	6	24	6	100
10	2×10^4	3	4	9	16	1	100

Characterization of the Diatoms

Subsamples of each composite sample were removed, acid cleaned, washed, and mounted into permanent diatom slides following Johansen et al. (1982). We then examined diatoms using a Zeiss Axioskop photomicroscope with high-resolution Nomarski DIC optics. Relative density of species was determined using counts of 100 frustules/sample.

Soil Chemistry

Soil chemical and physical analyses were conducted by the Soil Testing Laboratory at Brigham Young University using standard methods (Soil Survey Staff 1962, Soil Conservation Service 1972). Analyses included percent gravel, soil texture (gravimetric method), pH (saturated paste), electrical conductivity, and percent organic matter (Walkley-Black method). Nitrate-N, calcium, magnesium, and sodium levels were determined from soluble extracts. Phosphorus and potassium were extracted using sodium carbonate via the Olsen method (standard for alkaline soils). Sodium absorption ratio (SAR) was calculated using levels of calcium, magnesium, and sodium.

Statistical Analysis

Several different biometric methods were used to detect patterns in the data. The 10 sites were clustered based on Jaccard's similarity (Goodall 1978) utilizing the unweighted group average method of cluster generation (Pielou 1984). Centered, standardized principal component analysis (Pielou 1984) was used to ordinate sites based on soil chemical and physical parameters. Finally, canonical correspondence analysis (CCA) was used to simultaneously ordinate sites, species, and environmental variables (Ter Braak 1986, 1987). Normally, quantitative data are used for CCA analyses. Although we had quantitative data for diatoms, we had none for all other algae. To increase resolution of the CCA, we recorded 0 for absence, 1 for a single isolation from a site, and 2 for 2 or more isolations from a site. For diatom taxa, we recorded 0 for absence, 1 for relative abundances of 1–15%, and 2 for relative abundances >15%. CCA was run with full species data sets and then subsequently run with shortened sets. The taxa eliminated in short sets were those which did not vary in number in 9 or more sites.

RESULTS

Floristics

The total concentration of algae in the 10 locations within the study site ranged from 6×10^3 to 5×10^4 CFU/g soil (Table 2). Microbiotic crust cover was obvious at all sites, with the majority of sites showing 80–100% cover. Perennial vascular plant diversity was low, with only 1–6 species recorded from each area (Table 2).

A total of 66 algal species representing 32 genera were recovered from these sites (Table 3). Some widespread taxa were found in 8 or more sites. These common taxa included the cyanophytes *Nostoc commune* and *Schizothrix calcicola*, the chlorophyte *Myrmecia astigmatica*, and the diatoms *Hantzschia amphioxys*, *Hantzschia amphyoxys* f. *capitata*, *Luticola*

TABLE 3. Algal distribution in 10 sites from the Cataviña region of the Central Desert of Baja California, Mexico. Categories: 1 = 1 isolate from the site, 2 = 2 or more isolates from the site. Relative density is given for diatom taxa and chrysophyte cysts. Absence is indicated by a blank.

	Site									
Species	1	2	3	4	5	6	7	8	9	10
CYANOBACTERIA										
Anabaena sp.				1						
Lyngbya digueti Gom.						1				
Lyngbya putealis Mont.			1							
Microcoleus steenstrupii Boye-Pet.							1			
Microcoleus vaginatus (Vaucher) Gom.	1		1		1	1				
Myxosarcina burmensis Skuja				1						
Myxosarcina spectabilis Geitler						1				
Myxosarcina sp.					1					
Nostoc commune Vaucher	1		2	1	1	1	2	1	1	1
Nostoc muscorum Ag.					1					
Nostoc piscinale Kütz.		1	1				1			1
Nostoc punctiforme (Kütz.) Hariot				1	1	1	1			
Plectonema tomasinianum var. *gracile* Hansg.					1					
Plectonema sp.			1	1					1	
Schizothrix arenaria (Berk.) Gom.			1	1					1	
Schizothrix calcicola (Ag.) Gom.	2	2	2	2	1	2	2	2	2	2
Scytonema ocellatum Lyngb.				1						
Scytonema sp.	1			1			1			
CHLOROPHYTA										
Apatococcus constipatus (Printz) Printz	1		2				1			
Bracteacoccus aggregatus Tereg			1							
Bracteacoccus cohaerens Bischoff & Bold					1					
Bracteacoccus grandis Bischoff & Bold					1		1	1		
Bracteacoccus minor (Chodat) Petrová			1	1	1			2	1	
Bracteacoccus minutus Schwarz				1					1	1
Bracetacoccus pseudominor Bischoff & Bold								1		1
Chlorella ellipsoidea Gerneck							1			
Chlorella vulgaris Beijerinck		1		2			2			
Chlorococcum minutum Starr			1							
Chlorosarcinopsis aggregata Arce & Bold									1	
Chlorosarcinopsis arenicola Groover & Bold					1	1				
Chlorosarcinopsis auxotrophica Groover & Bold							1	1		
Chlorosarcinopsis bastropiensis Groover & Bold	1		1							
Chlorosarcinopsis gelatinosa Chant. & Bold	1	2	2							
Chlorosarcinopsis semipervirens Groover & Bold				1						
Cylindrocystis brebissonii var. *deserti*, sp. nov.							1			

cohnii, *Luticola mutica*, and *Pinnularia borealis* var. *scalaris*. Most taxa were rare, with 30 of the 66 species identified appearing in a single site. Although rare in our sites, most taxa isolated are species that commonly occur in desert soils. Notable exceptions (i.e., taxa not formerly found in desert soils of North America) include *Cylindrocystis brebissonii* var. *deserti*, *Elakatothrix obtusata*, *Elliptochloris subsphaerica*, *Fasciculochloris mexicana*, *Lobosphaeropsis lobophora*, *Lobosphaera tirolensis*, *Luticola muticoides*, and *Vischeria helvetica*. These taxa, unusual in desert soils, are described below. Three of them are new to science.

Cylindrocystis brebissonii var. *deserti*, var. nov.

(Figs. 1–9)

Coloniae prasini. Cellulae solitariae, cylindricae extremis rotundatus, 10–15 μm latae, 14–56 μm longae. Paries cellulae tenuis, pellucidus. Nucleus centralis. Chloroplastus elongatus porcis longitudinalibus lobatis, constrictus ad centrum partes duae formantes, unaquaeque pyrenoide; dimidia in cellulis aliqua axialibus. Pyrenoides plu minusve distincta granulis amylis, raro vagina amyla evidenti. Zygospora non observata.

Typus die April 1995 a solo deserti, locus 7, WHC #9579, lat. bor. 29°47′09.0″, long. occ.

TABLE 3. Continued.

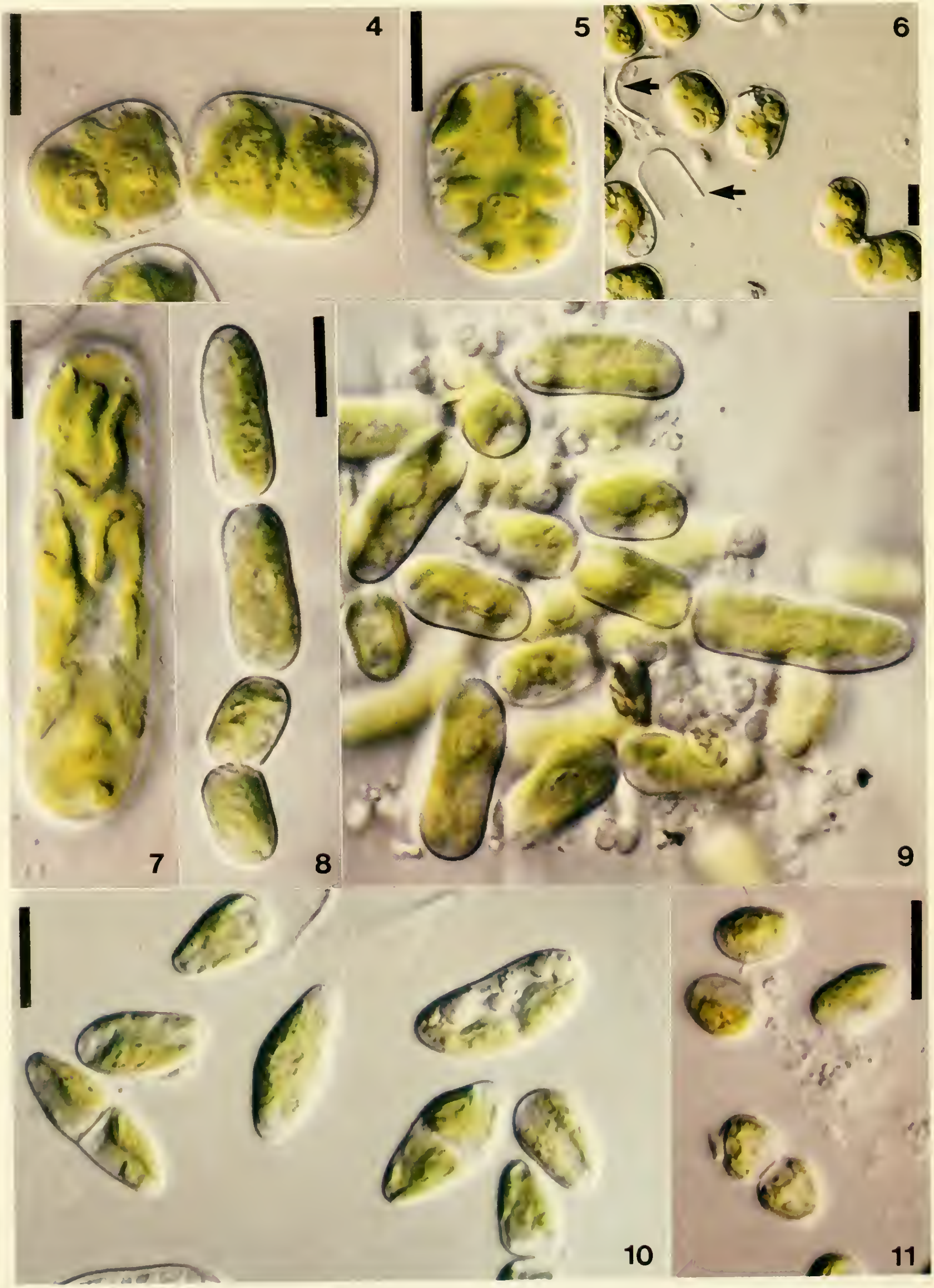
	Site									
Species	1	2	3	4	5	6	7	8	9	10
Dictyochloropsis splendida Geitler							1			
Diplosphaera species				1						
Elakatothrix obtusata, sp. nov.				1	1		1			
Elliptochloris subsphaerica (Reis.) Ettl & Gärt.		1								
Ettlia bilobata (Vinatzer) Komárek	1			1						
Ettlia cohaerens (Groover & Bold) Ettl & Gärt.				1					1	
Fasciculochloris mexicana, sp. nov.					1					
Klebsormidium dissectum (Gay) Ettl & Gärt.									1	1
Klebsormidium flaccidum (Kütz.) Sil., Matt. & Bl.							1			1
Lobosphaera tirolensis Reisigl			1	1	1					
Lobosphaeropsis lobophora (Andr.) Ettl & Gärt.									1	
Muriella decolor Vischer							1			
Muriella terrestris Boye-Pet.							1			
Myrmecia astigmatica Vinatzer		2	2	1		2		2	1	
Myrmecia biatorellae (Tsch. & Plessl) Boye-Pet.	1			1		1		1	1	
Myrmecia globosa Printz	1									
Myrmecia incisa Reisigl								1		
Myrmecia macronucleata (Deason) Andr.				1				1	1	
Spongiochloris minor Chant. & Bold								1	1	
Stichococcus bacillaris Nägeli				1						
EUSTIGMATOPHYTA										
Vischeria helvetica (Vischer & Pascher) Hibberd				2		1		1		2
BACILLARIOPHYTA (DIATOMS)										
Hantzschia amphioxys (Ehr.) Grunow	11	14	16	8	5	10	10	13	25	50
Hantzschia amphioxys f. *capitata* O. Müller	5	5	10	6	1	13	2	6	9	
Luticola cohnii (Hilse) Mann	34	24	41	33	24	13	33	19	25	19
Luticola mutica (Kütz.) Mann	30	38	32	33	38	32	32	33	35	20
Luticola muticoides (Hustedt) Mann							1			
Nitzschia hantzschiana Rabh.										1
Nitzschia punctata var. *minor* Temp. & Perag.			2							
Pinnularia borealis Ehr.		1			2			1		1
Pinnularia borealis var. *scalaris* (Ehr.) Rabh.	1			6	10		1	1	1	3
Staurosira construens (Ehr.) Williams & Round					1					
CHRYSOPHYTA										
Chrysophyte cysts	20	18	34	15	21	31	21	28	5	7

114°46′27.9″, Regio Catavińae, Desertum Centralis, California Inferna, Mexicum. Holotypus: BRY C 48041, Herbarium Cryptogamorum Nonvascularium, Brigham Young University, Provo, Utah. Isotypus in statu vivo: BC 9-8, UTEX Congeries Culturarum, University of Texas, Austin, Texas.

Colonies vivid grass green. Cells solitary, cylindrical with rounded ends, 10–15 μm wide, 14–56 μm long. Cell wall thin, clear. Nucleus central. Chloroplast elongated with longitudinal, lobed ridges, constricted in the center to form 2 halves, each with a pyrenoid, these halves appearing axial in some cells. Pyrenoids more or less distinct, with starch grains, rarely with an evident starch sheath. Zygospores not observed.

Type collected in April 1995 from desert soil surface, Site 7, WHC #9579, 29°47′09.0″ N latitude, 114°46′27.9″ W longitude, Cataviña region, Central Desert, Baja California, Mexico. Holotype: BRY C 48041, Herbarium of Nonvascular Cryptogams, Brigham Young University, Provo, Utah. Living isotype: BC 9-8, UTEX Culture Collection, University of Texas, Austin, Texas.

This taxon is very similar to the nominate variety of *C. brebissonii* Menegh. in terms of its chloroplast morphology and general shape (Figs. 5, 7). It differs in its smaller size. It is most similar to *C. brebissonii* var. *minor* West et West, which has a size range similar to var. *deserti* but differs in its slightly different chloroplast structure. The chloroplast of *C.*



Figs. 4–11. *Cylindrocystis brebissonii* var. *deserti* and *Elakatothrix obtusata* (scale = 10 µm). Figs. 4–7. *C. brebissonii* var. *deserti*. 4, vegetative cell division (note starch sheath around pyrenoids); 5 and 7, chloroplast showing lobed ridges and 1 pyrenoid; 6, persistent cell walls following cell division (arrows) and oblique cell division (right). Figs. 8–11. *E. obtusata*: 8–9, short chain of vegetative cells; 10–11, vegetative cell division (note triangular shape of cells).

brebissonii var. *minor* is illustrated as being stellate (Dillard 1990, plate 24, fig. 6), while that of var. *deserti* is clearly elongated with longitudinal, lobed ridges (Fig. 7). However, in the smallest cells, the chloroplast of var. *deserti* can appear stellate (Fig. 4), and so the varieties could be confused. The most compelling argument for recognizing the new variety is the very distinct habitat differences. *Cylindrocystis brebissonii* var. *deserti* occurs in neutral to alkaline desert soils, while other varieties of this species are in acidic aquatic habitats. The distinct habitat differences have caused us to place relatively more importance on the minor morphological differences between the varieties. Sexual stages, which are important in delineating *Cylindrocystis* taxa, were not observed. Only a single isolate was obtained.

Elakatothrix obtusata, sp. nov.

(Figs. 8–11)

Colonia flavovirens. Mucus extracellulosus mollis diffusus, copiosus in culturis vetustioribus. Cellulae generaliter decrescentes ad extrema, ovales ad leviter triangulares, raro prope sphaerici, natura triangulari maxime evidenti confestim post divisionem, interdum curvatae; solitariae vel binatim, infrequenter in catenis brevibus; uninucleatae; 5–6.5 µm latae, 6–14 µm longae. Paries cellulosus tenuis. Chloroplastus parietalis elongatus hemicellulam vel cellulam complens, interdum fractus. Pryenoides indistincta. Reproductio non nisi per fabricam autosporarum.

Typus die April 1995 a solo deserti, locus 4, WHC #9576, lat. bor. 29°47′10.5″, long. occ. 114°46′10.5″, Regio Cataviñae, Desertum Centralis, California Inferna, Mexicum. Holotypus: BRY C 48042, Herbarium Cryptogamorum Nonvascularium, Brigham Young University, Provo, Utah. Isotypus in statu vivo: BC 6-4, UTEX Congeries Culturarum, University of Texas, Austin, Texas. Paratypus: BRY C 48043, Herbarium Cryptogamorum Nonvascularium, Brigham Young University, Provo, Utah. Paratypus in statu vivo: BC 7-1, UTEX Congeries Culturarum, University of Texas, Austin, Texas.

Colony yellow green. Extracellular mucilage soft, diffuse; copious in older cultures. Cells generally tapered at ends, oval to somewhat triangular, rarely nearly spherical, with triangular nature most evident immediately after division, occasionally curved; in singles or pairs, occasionally in short chains; uninucleate, 5–6.5 µm in diameter, 6–14 µm long. Cell wall thin. Chloroplast parietal, elongate, filling half to entire cell; occasionally fragmented. Pyrenoid indistinct. Reproduction only through autospore production.

Type collected April 1995 from desert soil surface, Site 4, WHC #9576, 29°47′10.5″ N latitude, 114°46′10.5″ W longitude, Cataviña region, Central Desert, Baja California, Mexico. Holotype: BRY C 48042, Herbarium of Nonvascular Cryptogams, Brigham Young University, Provo, Utah. Living isotype: BC 6-4, UTEX Culture Collection, University of Texas, Austin, Texas. Paratype location Site 5, 29°47′17.7″ N latitude, 114°46′16.2″ W longitude, Cataviña region, Central Desert, Baja California, Mexico. Paratype: BRY C 48043, Herbarium of Nonvascular Cryptogams, Brigham Young University, Provo, Utah. Living paratype: BC 7-1, UTEX Culture Collection, University of Texas, Austin, Texas.

Our species differs from other species in the genus in having much shorter cells, which are not as clearly tapered as is typical for the genus. *E. obtusata* is most similar to *E. gelatinosa*, which also possesses an amorphous mucilage and has cells somewhat longer and thinner (13–18 µm long by 3–6 µm wide compared to 6–14 µm long by 5–6.5 µm wide in *E. obtusata*). Because of its relatively small length-to-width ratio, *E. obtusata* is much stouter and less tapered than all other species in the genus.

Elliptochloris subsphaerica (Reisigl) Ettl & Gärtner 1995

(p. 424, fig. 127:a–c)

Colony spherical, slightly mounded, grass green, even at 6 mon. Cells cylindrical when young, occasionally slightly bent, up to 1.5 times as long as wide, 3–8 µm wide, 5–10 µm long; becoming ellipsoidal to spherical with age, spherical cells 8–18 µm in diameter. Chloroplasts typically single, parietal, with a central pyrenoid, usually touching the edge of the cell at only a few points, becoming lobed or dissected into several plastids with age, starch positive when treated with iodine. Reproduction only through autospore production.

This chlorophyte is distinctive because of its production of small cylindrical cells that eventually round out to become larger spherical cells.

Fasciculochloris mexicana, sp. nov.

(Figs. 12–16)

Colonia scabera sicca, substrato adhaerens, atroviridis. Cellulae dispositae in massis, fasciculus cubicis, vel tetratibus isobilateralibus; parietibus arcte adpressis in culturis juventibus; in culturis vetustioribus fere sphaerescentes et in muco inclusae; uninucleatae; 3.5–6.5 µm latae, 6–8.5 µm longae. Paries cellulosus tenuis firmus, spissescens ad 4 µm in culturis scenescentibus. Cytoplasma granularis, vacuolis contractilibus duabus visibilibus in cellulis juventibus. Chloroplasus parietalis, cellulam complens ubi maturus. Pyrenoides excentrica, granulis grandibus amyli consociata; solitaria in cellulis juventibus, aliquot in cellulis vetustioribus. Zoosporae 4–16 in quoque cellula materno, ellipsoideae parietibus flagellis binis circa aequalibus, 1–2 vacuolis contractilibus, (2.4)–3.2–4 µm latae, 5–8 µm longae. Stigma linearis, media ad anticum. Chloroplastus parietalis, in medio zoospora. Nucleus posticus.

Typus die April 1995 a solo deserti, locus 5, WHC #9577, lat. bor. 29°47′17.7″, long. occ. 114°46′16.2″, Regio Catavińae, Desertum Centralis, California Inferna, Mexicum. Holotypus: BRY C 48044, Herbarium Cryptogamorum Nonvascularium, Brigham Young University, Provo, Utah. Isotypus in statu vivo: BC 7-6, UTEX Congeries Culturarum, University of Texas, Austin, Texas.

Colony rough, dry, adherent, dark green. Cells arranged in masses, cubical packets, or isobilateral tetrads; with tightly appressed walls in young cultures, becoming nearly spherical and encased in extracellular mucilage in older cultures; uninucleate, 3.5–6.5 µm wide, 6–8.5 µm long. Cell wall thin, firm, becoming thickened to 4 µm in senescent cultures. Cytoplasm granular, with 2 contractile vacuoles visible in young cells. Chloroplast parietal, filling the cell when mature. Pyrenoid eccentric, associated with large starch granules; solitary in young cells, multiple in older cells. Zoospores 4–16 per mother cell, biflagellate, walled, ellipsoidal, with 1–2 contractile vacuoles, (2.4)–3.2–4 µm in diameter, 5–8 µm long. Flagella of approximately equal length. Stigma linear, median to anterior in position. Chloroplast parietal, median. Nucleus posterior.

Type collected in April 1995 from desert soil surface, Site 5, WHC #9577, 29°47′17.7″ N latitude, 114°46′16.2″ W longitude, Cataviña region, Central Desert, Baja California, Mexico. Holotype: BRY C 48044, Herbarium of Nonvascular Cryptogams, Brigham Young University, Provo, Utah. Living isotype: BC 7-6, UTEX Culture Collection, University of Texas, Austin, Texas.

The original description of the genus *Fasciculochloris* (McLean and Trainor 1965) cites packet formation by vegetative cell division in 2 or 3 planes, presence of an extracellular gelatinous matrix surrounding individual cells and cell packets, and production of walled zoospores with the average size of 4 × 7 µm and unequal flagella; 1 species, *F. boldii*, is included in the genus. Our isolate displays the generic characteristics of cell packets formed by vegetative cell division, mucilage surrounding both individual cells and cell packets, and production of walled zoospores with flagella that are longer than the body length and, at least in some cases, slightly uneven in length (10% difference). Comparison of agar-grown cultures of our isolate with *F. boldii* culture 1451 obtained from the UTEX culture collection revealed several differences, the most notable of which were mucilage production and zoospore morphology. Mucilage production in our isolate was copious and evident surrounding both individual cells and cell packets (Figs. 12, 13). Average cell diameter of vegetative cells was 6.4 µm not including the mucilage envelope and 8.9 µm including the envelope; the diameter of nonenveloped cells was slightly smaller than that reported in the literature (McLean and Trainor 1964). Cells from UTEX culture 1451 were approximately 7 µm in diameter; mucilage production was less pronounced than that observed in our isolate or evident in photographs in the original

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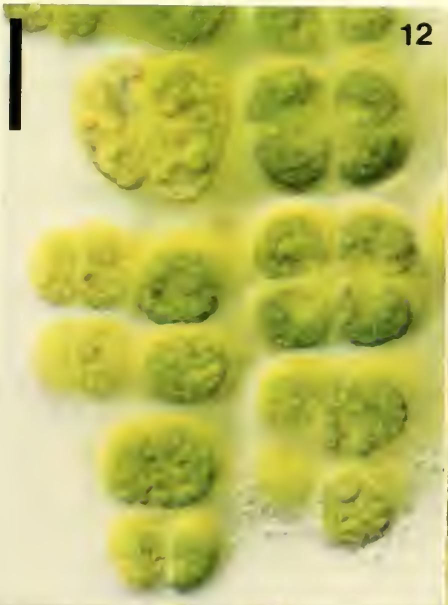
Figs. 12–25 (see facing page). *Fasciculochloris mexicana* and *Vischeria helvetica* (scale = 10 µm). Figs. 12–16. *F. mexicana:* 12, packet formation in vegetative cells; 13, cells embedded in extracellular matrix; 14–16, zoospore formation and morphology. Figs. 17–25. *V. helvetica:* 17–18, vegetative cells showing lobed chloroplast and prominent pyrenoid; 19, autospore formation; 20, mature cells showing carotenoid accumulation; 21, zoospores (note prominent stigma [arrow]); 22, young vegetative cell; 23, mature cell in early stages of orange pigment accumulation; 24, zoosporangium; 25, mature cell (note irregular cell shape).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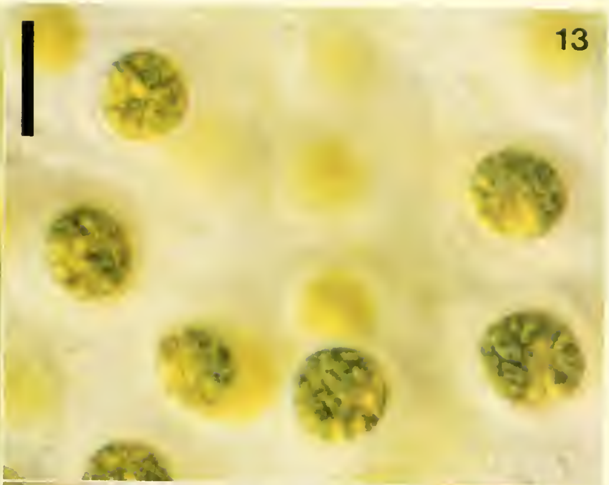
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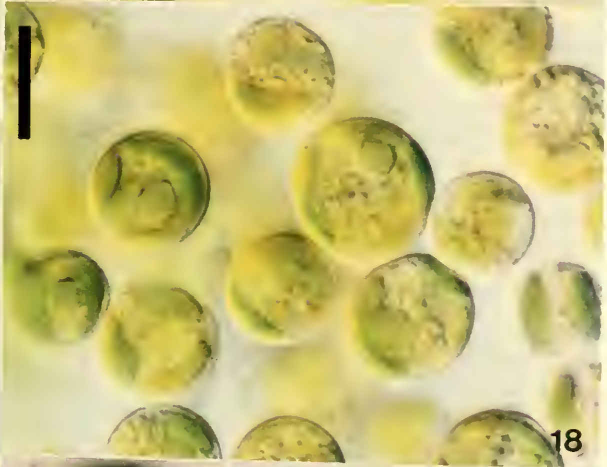
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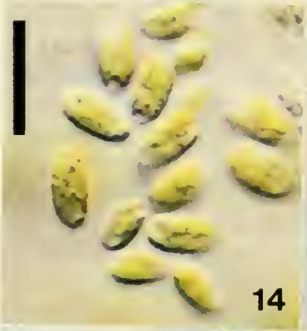
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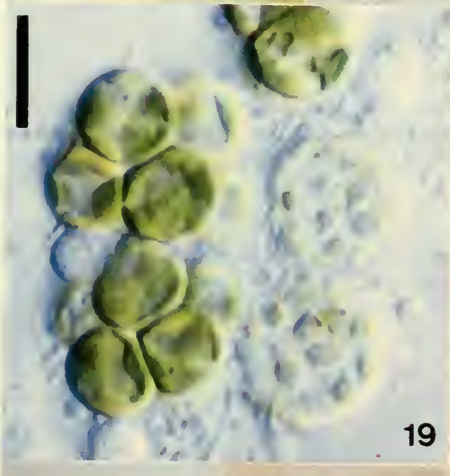
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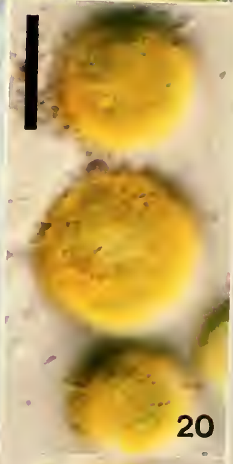
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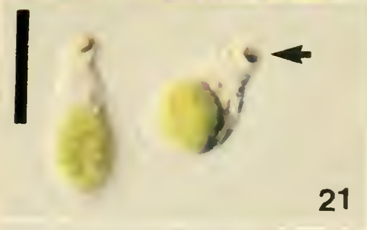
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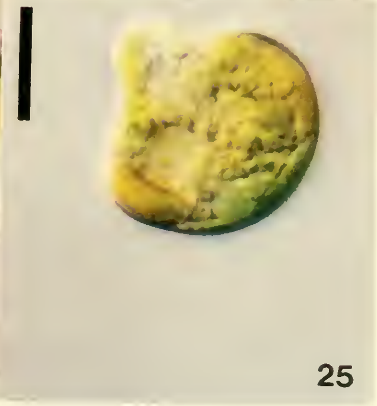
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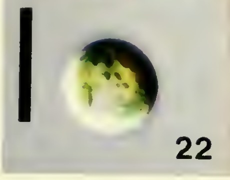
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publication. The most striking difference between our isolate and *F. boldii* is in zoospore morphology. The original description of *F. boldii* zoospores includes the presence of 2 contractile vacuoles, a median to posterior stigma, flagella of unequal length, and a size of 4 × 7 μm. Characteristics of the UTEX 1451 culture are generally consistent with the original description with the exception of size; zoospores of our subculture of the type material averaged 3 × 6 μm. The zoospores of our isolate had an average size of 3 × 5.3 μm and a clearly anterior stigma (Fig. 16). Length of the 2 flagella appeared approximately equal on some cells, but flagella which differed in length by approximately 10% (5.5 μm vs. 6.0 μm) were also observed. After extensive examination of glutaraldehyde-fixed cells, we feel confident in describing the flagella of our isolate as uneven, but less obviously so than the flagella of *F. boldii.*

Lobosphaeropsis lobophora
(Andreeva)
Ettl & Gärtner 1995
(p. 418, fig. 123:a)

Cells spherical to subspherical, uninucleate, 4–12 μm in diameter. Cell wall thin in young cells, thickening to 1 μm in older cells. Chloroplast parietal, becoming lobed, or sometimes filling the entire cell, with a clear pyrenoid. Oil droplets present, some cells with a slight orange pigment. Reproduction only through production of 2–4 autospores.

The genus *Lobosphaeropsis* was separated from *Chlorella* based on its lobed chloroplast (Reisigl 1969). It is distinct from *Lobosphaera* in that it possesses a pyrenoid.

Lobosphaera tirolensis
Reisigl 1964
(Ettl & Gärtner 1995,
p. 415, fig. 122:d)

Colony green to yellow green. Cells spherical or less often oval, in small groups, uninucleate, 6–16 μm in diameter. Cell wall thin. Chloroplast parietal, lobed, without a pyrenoid. Starch granules visible when stained with iodine. Reproduction only through autospore production.

Our isolates fit the morphological description for this species quite well, although the desert soil of Baja California is a very different habitat from the wet rocks and mosses in the Austrian Alps from which this species was described. We are concerned that with the disparity of habitats, our taxon may actually have a genetic identity quite different from the type of the species.

Luticola muticoides (Hustedt)
Mann in Round et al. 1990
(Hustedt 1961–66:598, fig. 1602)

Valves broadly elliptical-lanceolate, with rounded ends, 10–18 μm long, 6–7 μm wide. Raphe filiform, proximal ends clearly deflected to one side. Axial area broadened toward the center. Isolated punctum in a marginal or near marginal position on side opposite the side toward which raphe ends are deflected. Central area transverse, but generally not reaching the margins. Striae distinctly punctate, 22–24 in 10 μm.

The elliptical lanceolate shape, strongly deflected raphe ends, and marginal punctum separate this taxon from *Luticola mutica* and its varieties. Our specimens were more coarsely striated than those observed by Hustedt (1961–66).

Vischeria helvetica
(Vischer & Pascher) Hibberd 1981
(Ettl & Gärtner 1995:240,
fig. 61:c–e)

(Figs. 17–25)

Colony spherical, yellow green to olive. Cells spherical to oval, infrequently irregular, 8–22 μm in diameter. Cell wall thin. Chloroplast parietal, sometimes covering only 1 side of the cell, often lobed, with a square-cut pyrenoid, orange pigment often obvious, starch not present. A large vacuole with brownian movement of contents often present. Oil droplets evident in some cells. Reproduction through production of 2–4 autospores or through zoospore production. Zoospores flask-shaped, initially elongated, metabolic, 3.2–8 μm wide, 8–16 μm long, rounding up quickly. Chloroplast band shaped, covering 1/3 or less of the cell. Stigma eustigmatophyceaen; anterior, prominent, outside of chloroplast.

Characteristics of our strains are very similar to the description of *Eustigmatos magnus* (J.B. Petersen) Hibberd (1981). *E. magnus* is characterized as having spherical cells with a flexible, smooth cell wall, lobed parietal chloroplast,

TABLE 4. Soil chemistry analysis of 10 sites in the Central Desert of Baja California, Mexico. OM = organic matter, EC = electrical conductivity (µmhos/cm), SAR = sodium absorption ratio. Percent sand, silt, and clay were calculated after removal of gravel. Mineral nutrients in ppm.

	Site										
Parameter	1	2	3	4	5	6	7	8	9	10	Mean
pH	7.4	6.3	7.3	7.3	7.5	7.5	7.7	6.5	6.9	6.6	7.1
% gravel	10.0	16.0	22.0	21.0	35.0	11.0	9.0	11.0	15.0	9.0	15.9
% sand	80.8	77.1	66.6	73.3	57.6	78.1	87.9	80.1	79.1	75.1	75.6
% clay	8.2	11.4	14.4	11.7	22.4	8.2	6.4	9.9	8.9	10.2	11.2
% silt	11.0	11.5	19.1	15.0	20.1	13.7	5.7	10.0	12.0	14.7	13.3
% OM	0.5	0.6	0.6	0.8	0.4	0.6	0.4	0.5	0.7	0.4	0.6
NO_3	3.7	3.1	2.6	2.3	3.3	2.7	2.1	2.6	2.8	2.9	2.8
P	10.8	22.7	9.9	10.7	31.2	7.4	8.3	17.7	17.9	9.4	14.6
Exch. K	6.4	7.7	10.2	6.9	5.8	5.8	2.7	5.8	10.2	9.4	7.1
Sol. Ca	72.4	18.7	78.1	79.2	101.9	48.0	75.4	22.2	52.6	21.6	57.0
Sol. Mg	9.9	9.0	14.2	6.2	15.5	7.4	5.4	14.1	12.2	10.1	10.4
Sol. Na	49.6	16.0	26.2	5.4	37.4	24.8	1.6	17.8	9.6	12.3	20.1
EC	0.7	0.3	0.6	0.4	0.8	0.5	0.3	0.4	0.4	0.3	0.5
SAR	1.4	0.8	0.7	0.2	0.9	0.9	0.1	0.7	0.3	0.6	0.7

large vacuole, and angular pyrenoid. *Vischeria helvetica* shares the lobed chloroplast, angular pyrenoid, and in most cells, the thin, smooth cell wall and spherical shape. However, Hibberd (1981) states that at least some cells in a culture of spherical, smooth-walled cells are irregular or polyhedral. His illustration of *V. helvetica* (Hibberd 1981, fig. 10) is identical to our cells. The sizes of the 2 species are also similar, with our cells being more similar to the size range reported for *E. magnus*. Flagellated cells in *Vischeria* are unmentioned by Hibberd (1981) but illustrated in Ettl and Gärtner (1995). We did not observe the distinct ridges figured in the line drawings of *V. helvetica* (Ettl and Gärtner 1995). We decided to place our strains into *V. helvetica* based on the consistent presence of 3-cornered, angular cells and on the similarity in appearance to photomicrographs of the type culture (Hibberd 1981). If we are correct, our photomicrographs of the zoospores are the first to be published (Fig. 21). These taxa need further characterization, and we are not certain the distinction between *Eustigmatos* and *Vischeria* will persist when more strains of both are isolated and characterized.

Relationships Between Algal Distribution and Soil Variables

Clustering of sites on the basis of algal species revealed a low level of similarity among the sites, probably due to the extent of the rare taxa present. Sites 6 and 7 were most alike, showing 52% similarity; the remainder of site pairs had similarity indices of 29–44%. Because the sites clustered so poorly, this cluster is not shown.

Soil chemistry analyses reveal that the soils are sandy, have little organic matter (<0.8%), and have a pH in the neutral to slightly acidic range (Table 4). The greatest difference among soils is seen in the amount of phosphorus, potassium, calcium, and sodium. Comparison of the relative similarity of sites using PCA analysis based on soil chemistry showed little agreement with the clustering dendrogram based on floristic analysis. This finding suggests that differences in algal composition seen among the sites cannot be explained by the 14 soil variables examined.

To further explore the relationship between soil chemical and physical parameters and algal species distribution, we performed several canonical correspondence analyses (CCA). Most were uninformative. Since we had more environmental variables than sites, it was not appropriate to perform CCA with all environmental variables. Forward selection of environmental variables was conducted, and the following were selected: organic matter, K, electrical conductivity, percent gravel, Ca, Mg, and sodium absorption ratio. The shortened species list was used. This CCA did not agree with either the cluster analysis or the PCA based on soil chemistry. We interpret this to mean that correlations between combined soil chemistry parameters and algal species distribution are poor. Subsequent analyses utilized single environmental variables which

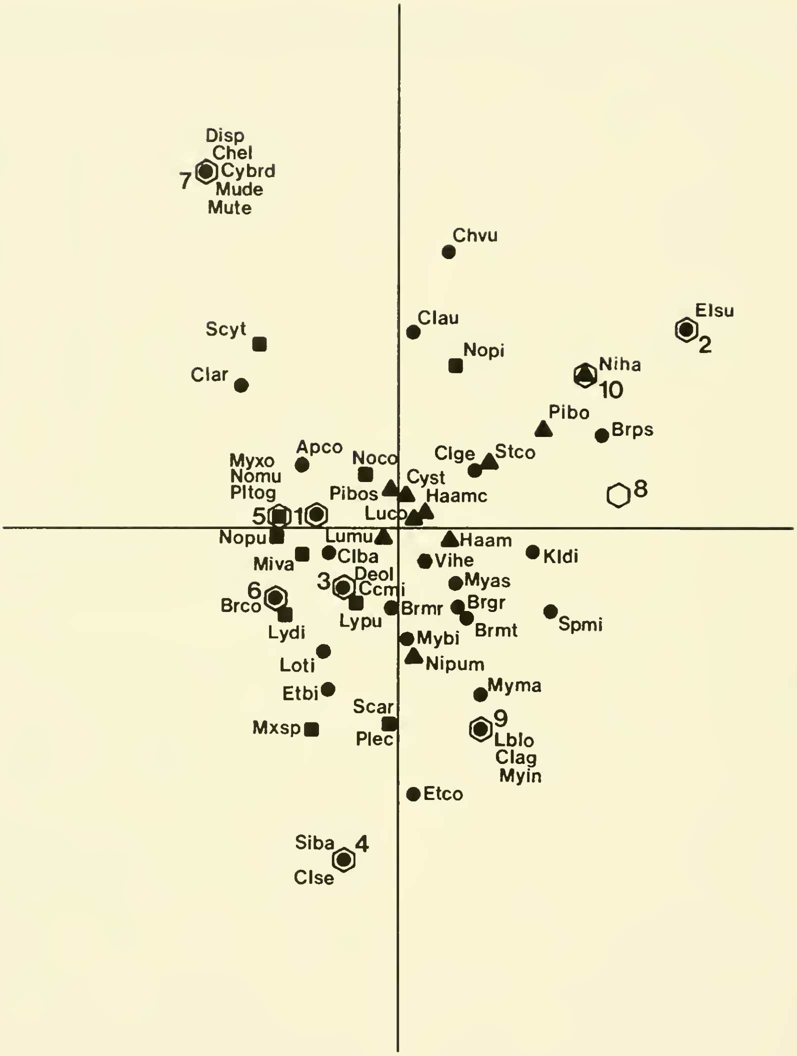

Fig. 26. Canonical correspondence analysis (CCA) of the 10 Cataviña sites when the axes were constrained to pH alone (all species used but not all shown). Axis 1 is negatively correlated with pH ($r = -0.962$); i.e., more alkaline samples are to the left, more acidic samples to the right. Eigenvalues for 1st and 2nd axes 0.250 and 0.386, respectively. Sites = hollow hexagons, cyanophytes = solid squares, chlorophytes = solid circles, diatoms and chrysophytes = solid triangles, eustigmatophytes = solid hexagon. Species codes consist of the first 2 letters of the genus, first 2 letters of the species, and first letter of the subspecific taxon, if given. With unknown species, the first 4 letters of the genus are given. Potentially confusing codes follow: Brmr = *Bracteacoccus minor*, Brmt = *Bracteacoccus minutus*, Ch = *Chlorella*, Cc = *Chlorococcum*, Cl = *Chlorosarcinopsis*, Cyst = chrysophyte cysts, Lo = *Lobosphaera*, Lb = *Lobosphaeropsis*, Lumu = *Luticola mutica*, My = *Myrmecia*, Mx = *Myxosarcina*, Sc = *Schizothrix*, Si = *Stichococcus*, St = *Staurosira*.

showed substantial variability among sites; these have been presumed to be important in the literature (pH, percent silt, sodium absorption ratio). Of these, only the CCA constrained to pH was informative (Fig. 26). Cyanobacterial taxa occurred in soils of higher pH, while chlorophyte and diatom taxa were distributed across the entire pH range. It is interesting to note that the *Myrmecia* species were found clustered together, suggesting they have similar pH requirements. Canonical correspondence analysis is less effective with the few sites used in this study, so these results should be interpreted with caution. However, CCA does appear to be a promising ordination method for soil algae. Apart from pH, we can see no trends that clearly connect algal species distribution in the Cataviña sites to soil chemical and/or physical parameters.

DISCUSSION

This study demonstrates that when a variety of methods are used to characterize the community, a high level of algal diversity can be detected in desert soils. We identified a total of 66 species. In past studies of desert soil algae, many investigators have concentrated their efforts on identifying cyanobacteria and diatoms (Cameron 1960, 1964, Durrell 1962, Shields and Drouet 1962, Hunt and Durrell 1966, Anderson and Rushforth 1976, Johansen et al. 1981, 1984, Ashley et al. 1985, Johansen and Rushforth 1985, Johansen and St. Clair 1986). The absence of careful chlorophyte and xanthophyte characterization is likely due to both the difficulty of their identification (which requires unialgal culture) and the lack of comprehensive taxonomic treatments prior to 1980. In general, when non-diatom eukaryotic algae were identified, it was only to the genus level (Martin 1939, Cameron 1960, Cain 1964, Friedmann et al. 1967, Archibald and Bold 1975, Metting and Rayburn 1979). Cameron (1964) attempted to identify non-diatom eukaryotic algae from the Sonoran Desert in southern Arizona, but identified only 9 species. Johansen et al. (1993) observed a total of 72 algal taxa from a single site in the Lower Columbia Basin, Washington, which was sampled seasonally for 12 mon. They observed 47 chlorophytes and 9 xanthophytes, many of which were identified to species. It is interesting to note that the latter study, employing methods identical to those used in this study, had nearly identical numbers of taxa, even though the floras demonstrated striking differences in composition.

This study is the most comprehensive floristic examination of soil algae from a geographically restricted hot desert community. The large number of species observed is due both to the variety of assay techniques used and the fact that 10 subsites within the area were studied. The observation that over 50% of the taxa were identified from a single site demonstrates compositional heterogeneity within desert soils. This finding also causes us to speculate that more extensive sampling in any one of our subsites would yield more taxa, and reinforces our contention that composite samples are a necessity given spatial heterogeneity in cryptogamic crust communities (Grondin and Johansen 1993).

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RESPONSE OF UNDERSTORY SPECIES TO CHANGES IN PONDEROSA PINE STOCKING LEVELS IN THE BLACK HILLS

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ABSTRACT.—The objective of this study was to test the hypothesis that there are no differences in understory production, by species, due to stocking levels of *Pinus ponderosa* (ponderosa pine). Understory production was estimated, by species, on 3 replicates each of 8 growing stock levels, ranging from clearcuts to unthinned stands, in both sapling- and pole-sized pine stands (48 plots) over 3 nonconsecutive years. All stands were approximately 70 yr old when thinning treatments were applied. Production of many herbaceous species, especially *Agropyron* spp. (wheatgrasses) and *Carex* spp. (sedges), declined as growing stock levels (measured in terms of basal area) of ponderosa pine increased. While trends in total production were similar, there were specific differences between sapling and pole stands. Sedges and *Oryzopsis asperfolia* (roughleaf ricegrass) produced more in sapling stands, whereas *Danthonia intermedia* (timber oatgrass) was more abundant in pole stands. Shrub production, dominated by *Arctostaphylos uva-ursi* (bearberry), was relatively consistent across all stocking levels except unthinned. Although the total number of species declined as pine basal area increased, a few species, such as *Linnaea borealis* (twinflower) and *Shepherdia canadensis* (buffaloberry), were found only under relatively dense pine canopies. While floristic species richness was greater at lower stocking levels of ponderosa pine, the total number of species would be greater if all stocking levels were present.

Key words: understory, ponderosa pine, Black Hills, plant species, biomass, production, stocking levels, floristic diversity.

Understory-overstory relationships have been studied extensively in *Pinus ponderosa* (ponderosa pine) stands in western North America (Ffolliott and Clary 1982). These studies have reported the response of forage classes, grasses and forbs, to overstory parameters such as canopy cover and basal area. Most have concluded that herbaceous understory vegetation exhibits greater growth when the competing overstory is reduced. Recent work on understory-overstory relationships in the Black Hills has related production of graminoids, forbs, and shrubs to various growing stock levels of *Pinus ponderosa* in both sapling and pole stands (Uresk and Severson 1989).

However, conventions governing management of public lands are changing. Emphasis is being placed on ecosystem management. This approach blends social, physical, economic, and biological needs and values to assure productive, healthy ecosystems (Kaufmann et al. 1994). Key features of ecosystem management are the protection and restoration of biodiversity, which Kaufmann et al. (1994) define as the variety of life and its processes, including variety in genes, species, and ecosystems, and the ecological processes that connect everything in ecosystems. Practical application of principles of ecosystem management will require more specific data. In the case of understory-overstory relationships, this means a better understanding of responses by plant species, rather than groups of species such as grasses, forbs, and shrubs.

The purpose of this paper is to describe how individual plant species responded to changes in basal area of *Pinus ponderosa* and to discuss how these responses could affect plant species richness in the understory of *Pinus ponderosa* forest in the Black Hills. This study was designed to test the null hypothesis that understory production does not differ by species due to changes in *Pinus ponderosa* growing stock levels.

STUDY AREA

The study was conducted on the Black Hills Experimental Forest, about 30 km west of Rapid City, South Dakota. The overstory within the experimental forest is dominated by *Pinus ponderosa*. Understory shrubs[2] include *Arctostaphylos uva-ursi* (bearberry), *Prunus*

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[2] Seedling trees were classified as shrubs for this study.

virginiana (common chokecherry), *Berberis repens* (Oregon grape), *Amelanchier alnifolia* (Saskatoon serviceberry), and *Symphoricarpos* spp. (snowberry). Common herbs include *Oryzopsis asperfolia* (roughleaf ricegrass), *Danthonia intermedia* (timber oatgrass), *Carex* spp. (sedges), *Poa pratensis* (Kentucky bluegrass), *Lathyrus ochroleucus* (cream peavine), and *Campanula rotundifolia* (bluebell). Most of the experimental forest is dominated by the *Pinus ponderosa/Arctostaphylos uva-ursi* habitat type (Hoffman and Alexander 1987) or HU-5, *Pinus ponderosa/Symphoricarpos alba/Arctostaphylos uva-ursi*, as described by Thilenius (1972).

The experimental forest encompasses about 1375 ha and elevations range from 1620 m to 1800 m. Average annual precipitation is 600 mm, 70% of which falls from April through September. Soils are primarily gray wooded, shallow to moderately deep, and derived from metamorphic rock (Boldt et al. 1983).

METHODS

Eight growing stock levels (GSL) of *Pinus ponderosa* including clearcuts and unthinned controls were sampled in both sapling- and pole-sized stands. These GSLs were numerically designated as 0, 5, 9, 14, 18, 23, 28 m^2 ha^{-1}, and unthinned. Growing stock indicates all living trees in a stand. Growing stock level is the basal area (m^2 ha^{-1}) of a stand adjusted to account for differences in the average size of trees left in the stand after thinning. Therefore, the numerical designation of GSL approximates, but does not necessarily equal, the actual basal area of the stand. Basal area of 0 m^2 ha^{-1} indicated clearcut plots. Average basal areas of unthinned pole stands ranged from 37 to 40 m^2 ha^{-1} in 1981, while unthinned sapling stands varied from 27 to 33 m^2 ha^{-1}. Three replicated plots were randomly assigned from a total of 48 plots and installed for each GSL from 5 to unthinned in sapling- and pole-sized stands in 1963. Stem diameters were 8–10 cm in sapling-sized stands, and 15–18 cm in pole-sized stands when treatments were installed. Three replicated clearcut plots in each of the sapling- and pole-sized stands were selected and treated in 1966. Cut material was removed from all plots. Each of the 24 plots in sapling stands was 0.1 ha and the 24 pole stands were each 0.2 ha. All GSLs were sampled in 1976; but budget restrictions resulted in sampling only 5 levels (0, 5, 14, 23 m^2 ha^{-1}, and unthinned) in 1974 and 1981.

Production of understory vegetation was measured during August 1974, 1976, and 1981 on six 15-m randomly placed transects per plot. Twelve 30 × 61-cm quadrats were randomly located along each transect in 1974 and 1976. These data indicated that an increase in number of quadrats would provide a better estimate of minor plant species. Therefore, in 1981, 25 circular plots measuring 0.125 m^2 each were systematically located along 5 of the transects. Current annual growth of all herbage was harvested at ground level for each species. All leaves and terminal portions of twigs to the first node were clipped on shrubs, also by species. Material was oven-dried at 60°C for 48 h and weighed. Weights were averaged and expressed as mean per plot for data analysis.

Heterogeneous variances were present, so data were transformed using a $\log_{(n)}+1$ transformation, analyzed with a one-way analysis of variance (years and stands analyzed separately) and means separated by Tukey's-HSD procedure. In those cases where heterogeneous variances persisted, means were separated using Dunnett's T3 (Dunnett 1980). Statistical inferences were made at a probability level of 0.1 for type I error to decrease type II error.

Plant nomenclature follows Great Plains Flora Association (1986) and Van Bruggen (1985).

RESULTS AND DISCUSSION

Several variables for this study were controlled to reduce variability. Effects of tree size class were separated, all plots were replicated 3 times on the same soil type and had similar site indices, all stands were approximately 70 yr old when treatments were applied, and data were collected over 3 separate years. High natural variability in the understory among replications was common despite this control. As a result, statistical tests often revealed nonsignificant differences despite widely separated means. The common occurrence of heterogeneous variances resulted in analysis via Dunnett's T3, a conservative test. Therefore, the standard error is as important as the mean values in the tables, especially values for individual species.

Relationships between overstory and general categories of understory (graminoids, forbs,

TABLE 1. Understory production (kg ha^{-1}, oven-dried basis) for 1974 in sapling-sized ponderosa pine stands growing at different tree stocking levels, Black Hills, South Dakota. Numbers are means ± standard errors. Values within a row followed by different letters are significantly different at the 0.10 probability level.

		Growing stock levels (m^2 ha^{-1})			
	Clearcuts	5	14	23	Unthinned
GRAMINOIDS					
Agropyron caninum	204 ± 100	73 ± 43	7 ± 4		<1
Bromus marginatus	1 ± 1				
Bromus porteri		2 ± 2			
Carex spp.	239 ± 123^{a}	335 ± 232^{a}	25 ± 5^{b}	5 ± 4^{b}	4 ± 2^{b}
Danthonia intermedia	19 ± 7	47 ± 20	47 ± 2	11 ± 5	2 ± 1
Elymus spp.				2 ± 2	
Festuca octoflora			<1		
Koeleria pyramidata	8 ± 4				
Oryzopsis asperifolia	144 ± 41^{ab}	304 ± 44^{a}	124 ± 88^{ab}	62 ± 48^{b}	30 ±5^{b}
Oryzopsis pungens			3 ± 3		
Poa pratensis	60 ± 42	42 ± 23			
Poa interior		3 ± 3	5 ± 5		<1
Schizachne purpurascens			1 ± 1		
Total	676 ± 110^{a}	806 ± 231^{a}	212 ± 91^{ab}	81 ± 41^{b}	36 ± 4^{b}
FORBS					
Achillea millefolium	57 ± 21	30 ± 14	2 ± 1	1 ± 1	<1
Agoseris glauca	1 ± 1				
Anaphalis margaritacea				2 ± 2	
Antennaria neglecta		3 ± 2	1 ± 1	1 ± 1	<1
Apocynum androsaemifolium		<1		<1	<1
Artemisia spp.	<1				
Aster spp.	<1				
Aster laevis	<1		<1	1 ± 1	
Astragalus adsurgens	5 ± 5				
Astragalus alpinus		8 ± 4	12 ± 6	1 ± 1	2 ± 2
Astragalus tenellus			1 ± 1		
Campanula rotundifolia	5 ± 3	11 ± 4	<1	<1	

shrubs, and total) aboveground biomass production were previously reported (Uresk and Severson 1989).

Graminoid Response

Carex spp., *Oryzopsis asperfolia*, and *Agropyron caninum* were the most productive species under sapling stands (Tables 1–3). Only *Carex* spp. and *Oryzopsis asperfolia* produced significantly more herbage at GSL 14 m^2 ha^{-1} and below. *Poa pratensis* and *Danthonia intermedia* were also common under saplings but biomass of both was lower. Only *Oryzopsis asperfolia* and *Danthonia intermedia* were common in GSLs above 18 m^2 ha^{-1}. Trends noted in pole-sized stands were somewhat similar (Tables 4–6). One of the most important differences between sapling and pole stands, however, was that *Carex* spp. and *Oryzopsis asperfolia* produced relatively less in pole stands than in sapling stands, whereas *Danthonia intermedia* produced more, particularly in clearcuts. As in sapling stands, significant differences by species among GSLs were rare. Only *Carex* spp. were found to produce more at lower GSLs in 1981 (Table 6).

The general responses of graminoids in both sapling and pole stands were similar to other Black Hills studies that included data on species (Pase 1958, Wrage 1994). Pase (1958) limited descriptions to the most important species (the rest were combined into an "other" category); but Wrage's descriptions (1994) were complete. Pase's study included a variety of sites throughout the Black Hills; and Wrage's study area, on soils similar to ours but a different habitat type, was about 10.5 km SE and 350 m lower in elevation than the experimental forest where this study was conducted.

Both studies reported responses similar to those herein, but some important differences were evident. Pase (1958) found that significant

TABLE 1. Continued.

		Growing stock levels (m^2 ha^{-1})			
	Clearcuts	5	14	23	Unthinned
Cirsium spp.	36 ± 36				
Delphinium bicolor	<1				
Erigeron spp.	3 ± 3	<1			<1
Fragaria vesca	9 ± 5	9 ± 7	4 ± 3	2 ± <1	<1
Galium boreale	3 ± 3				<1
Lactuca spp.		<1	1 ± 1		
Lathyrus ochroleucus	5 ± <1^{a}	27 ± 5^{b}	12 ± 7^{ab}	7 ± 4^{ab}	1 ± <1^{a}
Linnaea borealis				17 ± 17	<1
Oxytropis sericea				<1	
Solidago spp.			<1		
Taraxacum officinale	<1	<1	<1		
Vicia americana	<1	<1	<1		<1
Viola spp.	8 ± <1	12 ± 10	1 ± <1	1 ± <1	1 ± <1
Zizia aptera	<1				
Total	134 ± 39^{a}	102 ± 16^{ab}	37 ± 14^{ab}	34 ± 22^{ab}	8 ± 4^{b}
SHRUBS					
Amelanchier alnifolia	3 ± 2			1 ± <1	
Arctostaphylos uva-ursi	244 ± 74	205 ± 56	293 ± 78	255 ± 48	50 ± 7
Berberis repens				8 ± 8	
Populus tremuloides	1 ± 1	<1	<1	<1	<1
Rosa woodsii	7 ± 3	7 ± 5	4 ± 3	4 ± <1	1 ± <1
Rubus idaeus	28 ± 23	23 ± 7	5 ± 4		
Shepherdia canadensis				9 ± 9	
Spiraea betulifolia	2 ± 2	1 ± <1	1 ± <1	4 ± 2	1 ± <1
Symphoricarpos spp.	18 ± 8	7 ± 2	4 ± 3	3 ± 1	1 ± <1
Vaccinium scoparium				21 ± 21	
Total	303 ± 108^{a}	244 ± 57^{a}	308 ± 76^{a}	305 ± 20^{a}	54 ± 6^{b}
GRAND TOTAL	1113 ± 115^{a}	1152 ± 196^{a}	557 ± 138^{ab}	420 ± 57^{b}	98 ± 11^{c}

amounts of *Oryzopsis asperfolia* persisted under moderately dense canopy cover (40–59%, 19–27 m^2 ha^{-1} basal area) and dense canopy cover (60–71%, 28–33 m^2 ha^{-1} basal area), which compared with our findings. Pase (1958) and Wrage (1994) used canopy cover in their papers; we converted these to basal area estimates using Bennett's (1984) model: % canopy cover = 0.51BA(ft^2 ac^{-1}) – 1.94, R^2 = 0.83. Wrage (1994) did not find *Oryzopsis asperfolia* in his plots. Both Pase and Wrage noted that *Danthonia* (oatgrass) was most abundant under intermediate pine canopies. We found the same relationship under sapling stands, but in pole stands *Danthonia* was more abundant in clearcuts than in other GSLs. *Poa*, the most abundant grass component in open stands studied by both Pase and Wrage, was common but subdominant in this study. Pase (1958) listed *Poa pratensis*, *Sporobolus heterolepis* (prairie dropseed), and *Carex* spp. as the most common graminoids in pine cover class 0–19% (0–9 m^2 ha^{-1} basal area). Wrage (1994) listed *Poa*, *Carex* spp., and the exotic *Bromus inermis* (smooth brome) as being most common in open stands (<30% pine cover, 14 m^2 ha^{-1} basal area). We found *Agropyron caninum*, *Carex* spp., and *Oryzopsis asperfolia* most abundant in 0 and 5 GSL sapling stands and *Danthonia*, *Carex* spp., and *Agropyron caninum* most abundant in pole stands.

We considered 11 species as uncommon in sapling stands, defining uncommon as producing <5 kg ha^{-1} in ≤3 stands over all years (Tables 1–3). Included among these were *Bromus marginata* (mountain brome), *Schizachne purpurascens* (false melic), *Oryzopsis pungens* (mountain ricegrass), and the exotic *Agropyron cristatum* (crested wheatgrass). There were 10 uncommon graminoid species in the understory of pole-sized stands (Tables 4–6). Two of these, *Bromus marginatus* and *Oryzopsis*

TABLE 2. Understory production (kg ha^{-1}, oven-dried basis) for 1976 in sapling-sized ponderosa pine stands growing at different tree stocking levels, Black Hills, South Dakota. Numbers are means ± standard errors. Values within a row followed by different letters are significantly different at the 0.10 probability level.

		Growing stock levels (m^2 ha^{-1})						
	Clearcuts	5	9	14	18	23	28	Unthinned
GRAMINOIDS								
Agrostis stolonifera	<1	2 ± 2	2 ± <1	1 ± 1		<1	<1	<1
Agropyron caninum	144 ± 81	101 ± 64	100 ± 22	26 ± 20	18 ± 9			<1
Carex spp.	595 ± 290	261 ± 228	55 ± 37	49 ± 10	28 ± 17	8 ± 4	10 ± 7	14 ± 7
Danthonia intermedia	36 ± 20	67 ± 22	87 ± 36	77 ± 13	55 ± 28	41 ± 14	3 ± 2	1 ± <1
Koeleria pyramidata					<1			
Oryzopsis asperifolia	71 ± 46	311 ± 160	83 ± 45	298 ± 182	107 ± 43	67 ± 15	26 ± 11	42 ± 19
Oryzopsis pungens	2 ± 1	3 ± 3	2 ± 1	<1	4 ± 4	<1		
Poa pratensis	19 ± 18	50 ± 16	12 ± 9	3 ± 3	3 ± 2			
Stipa comata						10 ± 10		
Unknown grass		<1						
Total	867 ± 247^{a}	796 ± 81^{a}	340 ± 79^{ab}	454 ± 187^{ab}	216 ± 74^{abc}	127 ± 18^{bc}	39 ± 19^{c}	57 ± 24^{c}
FORBS								
Achillea millefolium	133 ± 39	37 ± 19	30 ± 8	10 ± 7	6 ± 3	8 ± 5	2 ± 2	
Antennaria neglecta	4 ± 4	4 ± 2	4 ± 4	2 ± 2	1 ± 1	6 ± 4		<1
Apocynum androsaemifolium		<1	3 ± 1				<1	<1
Aster laevis	<1			<1				
Astragalus adsurgens	12 ± 6	41 ± 28	29 ± 9	17 ± 14	2 ± 2	6 ± 3	6 ± 2	2 ± 2
Campanula rotundifolia	34 ± 19	12 ± 6	<1		1 ± 1	<1		1 ± <1
Chenopodium capitatum			99 ± 99					
Cirsium spp.				6 ± 6				
Delphinium bicolor	<1		<1					
Erigeron subtrinervis	2 ± 2	11 ± 11	2 ± 2			<1		<1
Fragaria vesca	15 ± 4	5 ± 1	9 ± 3	3 ± 3	8 ± 3	<1	<1	2 ± 2
Galium boreale	31 ± 31		4 ± 2	2 ± 2	2 ± 1	1 ± 1		
Lathyrus ochroleucus	15 ± 4	113 ± 5	83 ± 14	23 ± 9	36 ± 7	20 ± 11	10 ± 5	7 ± 6
Solidago spp.			2 ± 2					

TABLE 2. Continued.

		Growing stock levels (m^2 ha^{-1})						
	Clearcuts	5	9	14	18	23	28	Unthinned
FORBS (continued)								
Taraxacum officinale	<1							
Trifolium repens	<1	3 ± 3	5 ± 5					
Unknown forb	20 ± 15	6 ± 5	5 ± 5	<1				
Vicia americana	17 ± 9	11 ± 2	22 ± 8	2 ± 2	2 ± 1			
Viola adunca	13 ± 2	5 ± 1	4 ± 4	3 ± 3	<1	<1	<1	1 ± 1
Total	296 ± 33^{a}	246 ± 38^{ab}	306 ± 86^{a}	64 ± 16^{abc}	59 ± 16^{abc}	43 ± 11^{bc}	19 ± 8^{c}	15 ± 9^{c}
SHRUBS								
Amelanchier alnifolia	<1	<1	9 ± 6	5 ± 3	6 ± 3	4 ± 3	<1	<1
Arctostaphylos uva-ursi	760 ± 354	1095 ± 411	1081 ± 255	753 ± 326	1243 ± 185	553 ± 344	787 ± 327	260 ± 114
Berberis repens			3 ± 3			10 ± 10		1 ± 1
Populus tremuloides	98 ± 81		<1	<1				
Prunus virginiana					1 ± 1		<1	
Rosa woodsii	9 ± 3^{ab}	18 ± 12^{a}	10 ± 3^{ab}	9 ± 5^{ab}	7 ± <1^{b}	6 ± 2^{b}	1 ± <1^{b}	2 ± <1^{b}
Rubus idaeus	70 ± 70^{a}	29 ± 12^{ab}	45 ± 6^{a}	4 ± 4^{b}	6 ± 4^{b}			<1^{b}
Shepherdia canadensis			85 ± 85			7 ± 7		
Symphoricarpos spp.	24 ± 15	14 ± 12	23 ± 1	7 ± 5	5 ± 3	3 ± 1	2 ± 1	1 ± <1
Unknown shrub	2 ± 2							
Vaccinium scoparium						14 ± 14		4 ± 4
Total	964 ± 411	1156 ± 54	1255 ± 233	778 ± 331	1267 ± 178	597 ± 330	791 ± 329	269 ± 111
GRAND TOTAL	2126 ± 196^{ab}	2199 ± 70^{a}	1901 ± 280^{ab}	1296 ± 128^{abc}	1542 ± 113^{abc}	1202 ± 327^{abc}	850 ± 342^{bc}	341 ± 138^{c}

TABLE 3. Understory production (kg ha^{-1}, oven-dried basis) for 1981 in sapling-sized ponderosa pine stands growing at different tree stocking levels, Black Hills, South Dakota. Numbers are means ± standard errors. Values within a row followed by different letters are significantly different at the 0.10 probability level.

		Growing stock levels (m^2 ha^{-1})			
	Clearcuts	5	14	23	Unthinned
GRAMINOIDS					
Agropyron cristatum			1 ± 1		
Agropyron spicatum		9 ± 9			
Agropyron caninum	282 ± 48	74 ± 19	24 ± 24	6 ± 4	
Bromus marginatus			<1		
Carex spp.	508 ± 232^{a}	429 ± 160^{a}	105 ± 56^{ab}	26 ± 13^{b}	15 ± 13^{b}
Danthonia intermedia	48 ± 8	141 ± 27	49 ± 16	15 ± 11	4 ± 3
Festuca ovina		<1	1 ± >1		
Koeleria pyramidata	1 ± >1	3 ± 3			
Oryzopsis asperifolia	176 ± 8^{ab}	393 ± 49^{a}	237 ± 121^{a}	70 ± 17^{b}	59 ± 24^{b}
Oryzopsis pungens	2 ± 2			1 ± 1	
Poa pratensis	252 ± 67	1 ± 1			
Poa interior	27 ± 18	16 ± 7		<1	
Unknown grass	1 ± 1	23 ± 0	2 ± 2		<1
Total	1297 ± 263^{a}	1089 ± 142^{a}	424 ± 177^{ab}	118 ± 15^{b}	79 ± 35^{b}
FORBS					
Achillea millefolium	88 ± 42	52 ± 17	9 ± 4	3 ± 3	2 ± 1
Agoseris glauca	14 ± 6				
Antennaria neglecta	2 ± 2	5 ± 3	1 ± 1	2 ± 1	1 ± <1
Apocynum androsaemifolium	<1	3 ± 2	2 ± 1	5 ± 4	1 ± 1
Astragalus canadensis			3 ± 2		
Astragalus adsurgens	20 ± 4	17 ± 6	4 ± 3	3 ± 3	2 ± 2
Astragalus spp.		1 ± 1		<1	
Astragalus tenellus	12 ± 6	6 ± 3	5 ± 5	5 ± 5	5 ± 5
Campanula rotundifolia	25 ± 5	8 ± 2	1 ± 1		<1
Cirsium vulgare	17 ± 13	1 ± 1		<1	
Delphinium bicolor					<1
Erigeron spp.	5 ± 5	1 ± <1	<1	<1	
Fragaria vesca	33 ± 2^{a}	24 ± 15^{ab}	7 ± 5^{b}	3 ± <1^{b}	2 ± 1^{b}

pungens, also occurred in sapling stands. Others included *Koelaria cristata* (prairie junegrass), which was common in sapling stands, *Poa arida* (plains bluegrass), *Bromus porteri* (nodding brome), and the exotic *Phleum pratense* (timothy). All uncommon species occurred in pine stands stocked at ≤14 m^2 ha^{-1} basal area. Wrage (1994: Appendix D) had 8 grass species that contributed <1% foliar cover in ≤3 stands over all years and all *Pinus ponderosa* cover classes: *Agropyron repens* (quackgrass), *A. intermedium* (intermediate wheatgrass), *Bouteloua curtipendula* (sideoats grama), *Calamagrostis rubescens* (pine reedgrass), *Muhlenbergia torreyi* (ring muhly), *Schizachne purpurascens*, *Sporobolus asper* (rough dropseed), and *Stipa spartea* (porcupine grass).

Three exotic grasses were found under the pine overstory; one, *Agrostis stolonifera* (redtop), was common but scattered. The others, *Agropyron cristatum* and *Phleum pratense*, occurred only in a single stand each. *Poa pratensis* was not considered exotic because it occurs in both naturalized and native forms in this area (Great Plains Flora Association 1986). Wrage (1994) reported 3 exotic grasses: *Agropyron repens*, *Agropyron intermedium*, and *Bromus inermis.*

Altogether, we found and identified 22 different graminoids in the pine understory in this study. Thirteen were common to sapling- and pole-sized stands while 3 and 2 species were unique to each respective size class. Pase (1958) reported 38 graminoid species and Wrage (1994) listed 23.

An average of 9 graminoid species occurred in GSLs 0, 5, and 14 m^2 ha^{-1} over all years. This was higher ($P < 0.05$) than the 6 and 5 species found in GSL 23 and unthinned stands, respectively (Uresk and Severson 1989). The mean number of species present in pole clearcuts (11) and GSL 5 m^2 ha^{-1} (10) was

TABLE 3. Continued.

		Growing stock levels (m^2 ha^{-1})			
	Clearcuts	5	14	23	Unthinned
Galium boreale	18 ± 13	1 ± 1	2 ± 2		<1
Hieracium canadense		<1		1 ± 1	
Iris missouriensis		<1			
Lathyrus ochroleucus	40 ± 20	117 ± 28	68 ± 33	39 ± 13	10 ± 6
Linnaea borealis			<1	2 ± 2	<1
Lupinus spp.	3 ± 3			7 ± 4	
Monarda fistulosa	1 ± 1			1 ± 1	
Polygonum persicaria	1 ± 1				
Smilacina stellata			2 ± 2		
Solidago sparsiflora	7 ± 4	6 ± 5	<1	11 ± 11	<1
Taraxacum officinale	1 ± 1	<1			
Trifolium repens	1 ± 1	4 ± 4		11 ± 11	<1
Vicia americana	57 ± 35^{a}	12 ± 2^{b}	9 ± 9^{b}	2 ± 2^{b}	1 ± 1^{b}
Viola adunca	25 ± 1	18 ± 3	2 ± 2	1 ± 1	1 ± 1
Total	369 ± 99^{a}	276 ± 6^{a}	117 ± 52^{abc}	92 ± 10^{bc}	26 ± 16^{c}
SHRUBS					
Amelanchier alnifolia	2 ± 1		1 ± 1	1 ± 1	<1
Arctostaphylos uva-ursi	604 ± 179	820 ± 95	872 ± 427	821 ± 333	205 ± 111
Berberis repens				8 ± 8	4 ± 4
Populus tremuloides	1 ± 1		3 ± 3		
Rosa woodsii	25 ± 2	21 ± 12	13 ± 8	11 ± 6	3 ± 3
Rubus idaeus	130 ± 117	61 ± 24	22 ± 13	1 ± 1	3 ± 3
Shepherdia canadensis				9 ± 9	7 ± 7
Spiraea betulifolia	1 ± 1	1 ± <1	7 ± 2	8 ± 4	4 ± 2
Symphoricarpos spp.	38 ± 10	12 ± 4	20 ± 13	5 ± 3	3 ± 2
Vaccinium scoparium				1 ± 1	
Total	802 ± 307	915 ± 126	938 ± 428	866 ± 326	230 ± 107
GRAND TOTAL	2450 ± 168^{a}	2280 ± 102^{a}	1478 ± 596^{ab}	1076± 330^{ab}	334 ± 146^{b}

greater ($P < 0.05$) than the 5, 5, and 3 species found in GSLs 14, 23, and unthinned stands, respectively (Uresk and Severson 1989). Wrage (1994) counted 20, 19, and 16 grass species in his open (tree cover <30%, 14 m^2 ha^{-1} basal area), intermediate (30–60%, 14–27 m^2 ha^{-1}), and dense (>60%, 27 m^2 ha^{-1}) *Pinus ponderosa* stands, respectively.

Forb Response

Forb response, relative to GSLs, was similar to that of graminoids except that forbs produced about 30% less forage (Tables 1–6). No single forb species dominated any GSL of either size class; however, *Achillea millifolium* (common yarrow), *Campanula rotundifolia*, and *Lathyrus ochroleucus* were the most common forbs found in pole stands (Tables 4–6). *Achillea millifolium* and *Lathyrus ochroleucus* were the most abundant forbs in sapling stands (Tables 1–3), but few significant differences by species among GSLs were noted. *Lathyrus ochroleucus* produced more herbage in mid-level GSL sapling stands (5–23) in 1974 (Table 1), and *Fragaria vesca* (woodland strawberry) and *Vicia americana* (American vetch) produced more in clearcuts in 1981 (Table 3), but no differences were noted in pole stands. Pase (1958) reported *Trifolium repens* (white clover), *Fragaria vesca*, and *Achillea millifolium* to be abundant in open stands, but only *Lathyrus ochroleucus* and *Solidago* spp. (goldenrod) persisted under moderately dense pine canopies. *Artemisia ludoviciana* (white sagewort), *Glycyrrhiza lepidota* (wild licorice), *Psoralea argophylla* (silverleaf scurfpea), and *Monarda fistulosa* (wild bergamot) were the most common forbs in Wrage's (1994) open stands, but only *Glycyrrhiza lepidota* persisted into intermediate stands. Forbs were scarce in his dense

TABLE 4. Understory production (kg ha^{-1}, oven-dried basis) for 1974 in pole-sized ponderosa pine stands growing at different tree stocking levels, Black Hills, South Dakota. Numbers are means ± standard errors. Values within a row followed by different letters are significantly different at the 0.10 probability level.

		Growing stock levels (m^2 ha^{-1})			
	Clearcuts	5	14	23	Unthinned
GRAMINOIDS					
Agrostis stolonifera	<1				
Agropyron spicatum	3 ± 2	<1			
Agropyron caninim	155 ± 89	3 ± 2	<1		
Bromus marginatus		<1			
Bromus porteri		2 ± 2	<1		
Carex spp.	7 ± 4	15 ± 9	2 ± <1	10 ± 5	<1
Danthonia intermedia	322 ± 21	135 ±31	46 ± 17	5 ± 2	
Festuca octoflora	20 ± 10	<1			
Festuca ovina	<1	2 ± 1			
Koeleria pyramidata	3 ± 3				
Oryzopsis asperifolia	9 ± 8	29 ± 24		17 ± 15	4 ± 3
Poa spp.	10 ± 4				
Poa pratensis	7 ± 4	4 ± 4			
Total	538 ± 76^{a}	193 ± 45^{ab}	48 ± 15^{b}	32 ± 17^{bc}	5 ± 4^{c}
FORBS					
Achillea millefolium	39 ± 11	6 ± 3	1 ± 1	1 ± 1	<1
Antennaria neglecta	7 ± 4	9 ± 9	9 ± 6	3 ± 2	
Apocynum androsaemifolium	<1	1 ± <1	<1	<1	<1
Astragalus alpinus	13 ± 3	17 ± 11	<1	1 ± 1	
Astragalus tenellus	4 ± 3	3 ± 3		3 ± 3	
Astragalus spp.	3 ± 3	<1	1 ± 1	<1	
Campanula rotundifolia	35 ± 22	6 ± 2		<1	
Cirsium arvense	14 ± 14				
Cirsium vulgare	15 ± 8				
Erigeron spp.	2 ± 1	4 ± 1	1 ± 1	<1	
Fragaria vesca	3 ± 2	<1	<1	<1	

stands; those most common were *Galium boreale* (northern bedstraw) and *Smilacina stellata* (false Solomon's seal).

Many forb species occurred under the pine canopy, but they contributed little to total aboveground biomass. We categorized 22 species as uncommon, using "uncommon" as we defined it for graminoids. Wrage (1994) also noted many forbs that were generally scarce. If we arbitrarily classify uncommon species in Wrage's study as those having <1% foliar cover in ≤3 pine cover classes over all years, 18 forb species would be considered uncommon (Wrage 1994: Appendix D).

Nine of the forbs found in the pine understory are exotic species. Only 2, however, were common: *Taraxacum officinale* (common dandelion) and *Trifolium repens*. These species are both ubiquitous over North America. Two others, both noxious weeds, *Cirsium arvense* (Canada thistle) and *C. vulgare* (bull thistle), were common only locally. Another, *Linaria vulgaris* (butter-and-eggs), was found only in pole clearcuts. The other 4, *Polygonum persicaria* (lady's thumb), *Tragopogon dubius* (goats beard), *Sisymbrium altissimum* (tumbling mustard), and *Rumex acetosella* (sheep sorrel), were rare. A large amount of *Chenopodium capitatum* (strawberry blite) was found in 1 plot of 1 replicate of sapling GSL 9 m^2 ha^{-1} in 1976 (Table 2). It is unknown whether this species is indigenous or exotic (Great Plains Flora Association 1986). Wrage (1994) listed 4 exotic species, *Cirsium arvense*, *Convolvulus arvense* (field bindweed), *Taraxacum officinale*, and *Tragopogon dubius*. All were classed as uncommon except *Convolvulus arvense*, which was common in open stands.

Although our aboveground biomass estimates of forbs were less than for graminoids, there were more forb species than graminoid species. Fifty-three forbs, including 15 identified only to genus, grew in the understory; 25 identified species were common to both

TABLE 4. Continued.

		Growing stock levels (m^2 ha^{-1})			
	Clearcuts	5	14	23	Unthinned
Galium boreale		<1		<1	
Iris missouriensis	1 ± 1		<1		
Lactuca spp.		5 ± 2	3 ± 1	8 ± 7	<1
Lathyrus ochroleucus	7 ± 6				
Linaria vulgaris	<1				
Oxytropis sericea		6 ± 4	9 ± 7	<1	
Potentilla spp.	<1				
Solidago spp.	3 ± 3	<1		1 ± 1	
Taraxacum officinale	<1	<1			
Trifolium repens	5 ± 5	23 ± 23		<1	
Vicia americana	2 ± 2	<1	<1	<1	
Viola spp.	5 ± <1	3 ± 2			
Total	161 ± 15^a	86 ± 35^{ab}	28 ± 5^b	22 ± 7^b	<1^c
SHRUBS					
Amelanchier alnifolia	1 ± 1	5 ± 5	<1		
Arctostaphylos uva-ursi	209 ± 7	305 ± 94	306 ± 72	135 ± 35	66 ± 58
Berberis repens		19 ± 19			
Betula papyrifera	<1				
Juniperus communis	<1				
Populus tremuloides	21 ± 21	<1			
Rosa woodsii	10 ± 8	<1	2 ± 2	<1	<1
Rubus idaeus	49 ± 17	10 ± 6			
Shepherdia canadensis				10 ± 10	
Spiraea betulifolia	1 ± <1	3 ± 2	<1	1 ± <1	
Symphoricarpos spp.	7 ± 7	3 ± 3	2 ± 2	2 ± 2	<1
Total	299 ± 48	347 ± 77	311 ± 70	149 ± 43	67 ± 58
GRAND TOTAL	998 ± 84^a	626 ± 46^b	387 ± 87^{bc}	203 ± 34^{bc}	72 ± 58^c

saplings and poles, while 6 and 7 species were unique to the sapling and pole understories, respectively. Pase (1958) and Wrage (1994) noted 63 and 41 forb species in their respective studies.

We found an average of 18 forb species over all years in clearcut sapling stands, which was significantly higher ($P < 0.05$) than the 15, 13, and 13 species found in GSLs 5, 14, and 23 m^2 ha^{-1}, respectively. Eleven species were found in unthinned stands, fewer ($P < 0.05$) than in clearcuts (Uresk and Severson 1989). Trends were similar in pole-sized stands. Twenty-one species were found in clearcuts and 18 in GSL 5, which was higher ($P < 0.05$) than the 12 and 13 found in GSLs 14 and 23. Fewest species (5) were found in unthinned pole stands (Uresk and Severson 1989). Wrage (1994) counted 36, 29, and 24 forbs in *Pinus* stands with open, intermediate, and dense canopy covers.

Shrub Response

Mean shrub production was similar across all *Pinus ponderosa* sapling stocking levels in 1976 and 1981 and in 1974 pole stands. In the remaining sapling (1974) and pole (1976, 1981) stands, all growing stock levels produced more shrubs than unthinned stands. In general, shrub production tended to be somewhat higher at mid-levels than in clearcuts and much higher than in unthinned stands, although differences among lower GSLs were not significant (Tables 1–6). *Arctostaphylos uva-ursi* accounted for most shrub production in all stands regardless of size class or stocking levels, but differences were not significant except in pole stands in 1981 (Table 6). Production of *Arctostaphylos uva-ursi* was 75–99% of total shrub production in sapling stands and 70–99% in pole stands. Lower percentages tended to occur in clearcuts. Higher proportions of *Rubus idaeus* (red raspberry) and *Symphoricarpos* spp. (snowberry) were found in clearcuts. *Rosa woodsii* and

TABLE 5. Understory production (kg ha^{-1}, oven-dried basis) for 1976 in pole-sized ponderosa pine stands growing at different tree stocking levels, Black Hills, South Dakota. Numbers are means ± standard errors. Values within a row followed by different letters are significantly different at the 0.10 probability level.

		Growing stock levels (m^2 ha^{-1})						
	Clearcuts	5	9	14	18	23	28	Unthinned
GRAMINOIDS								
Agrostis stolonifera	3 ± 2	1 ± <1	<1	1 ± <1			<1	
Agropyron caninum	71 ± 11	52 ± 22	14 ± 8	2 ± 2	6 ± 6		1 ± 1	<1
Carex spp.	52 ± 20	32 ± 21	8 ± 7	5 ± 3	25 ± 23	6 ± 3	<1	1 ± <1
Danthonia intermedia	406 ± 69	180 ± 58	116 ± 27	196 ± 17	70 ± 28	37 ± 19	32 ± 12	4 ± 3
Festuca ovina	10 ± 5	2 ± 1						
Oryzopsis asperifolia	70 ± 70	38 ± 38	12 ± 12		2 ± 2	5 ± 5		4 ± 2
Oryzopsis pungens	<1	5 ± 3	<1		8 ± 7	<1	<1	
Poa pratensis	23 ± 21	27 ± 25	<1		3 ± 3			
Stipa spp.			3 ± 3					
Unknown grass		3 ± 3	6 ± 6					
Total	633 ± 30^{a}	341 ±120^{ab}	162 ± 22^{b}	205 ± 18^{b}	114 ± 46^{bc}	48 ± 26^{c}	35 ± 14^{c}	10 ± 5^{c}
FORBS								
Achillea millefolium	121 ± 19	27 ± 23	<1	4 ± 4	1 ± <1	<1	1 ± 1	
Agoseris glauca					<1			
Antennaria neglecta	25 ± 10	15 ± 15	4 ± 1	7 ± 4	1 ± <1	5 ± 5	1 ± <1	<1
Apocynum androsaemifolium	5 ± 3	7 ± 6			<1			
Aster laevis	3 ± 3	4 ± 4	2 ± 2	5 ± 4	<1	<1	<1	
Astragalus adsurgens	37 ± 12	24 ± 12	20 ± 13	24 ± 12	6 ± 4	5 ± 4	8 ± 5	<1
Campanula rotundifolia	88 ± 34	8 ± 4	1 ± 1	1 ± 1	4 ± 3	<1		
Cirsium vulgare	20 ± 10	10 ± 10						
Delphinium bicolor	<1	<1						
Erigeron subtrinervis	10 ± 5		<1		<1		<1	
Frageria vesca	3 ± 2	1 ± 1	3 ± 2	1 ± 1	1 ± 1	<1	<1	
Galium boreale		<1			<1	<1		
Lathyrus ochroleucus	25 ± 8	36 ± 10	30 ± 13	18 ± 11	35 ± 12	10 ± 5	10 ± 2	2 ± 1
Linaria vulgaris	26 ± 24	<1						

TABLE 5. Continued.

	Clearcuts	Growing stock levels (m^2 ha^{-1})						Unthinned
		5	9	14	18	23	28	
FORBS (continued)								
Sisymbrium altissimum		1 ± 1						
Solidago spp.			1 ± 1					
Solidago missouriensis	6 ± 6							
Taraxacum officinale	2 ± <1	<1						
Tragopogon dubius	<1							
Trifolium repens	46 ± 9	6 ± 6		9 ± 6				
Unknown forb	41 ± 21	3 ± 1	7 ± 7	<1	<1			
Vicia americana	2 ± 2	8 ± 8	<1 ± <1	2 ± 1	5 ± 3	4 ± 4	1 ± 1	
Viola adunca	16 ± 11	13 ± 7	2 ± 2	<1 ± <1	<1		<1	
Total	477 ± 82^a	164 ± 36^{ab}	74 ± 33^b	73 ± 31^b	56 ± 23^b	27 ± 8^b	24 ± 5^b	3 ± 1^c
SHRUBS								
Amelanchier alnifolia	8 ± 3	11 ± 6	6 ± 3	4 ± 4	6 ± 4	2 ± 1	1 ± <1	1 ± <1
Arctostaphylos uva-ursi	687 ± 187	827 ± 428	1124 ± 279	934 ± 277	507 ± 186	675 ± 155	422 ± 145	96 ± 94
Berberis repens		65 ± 65			1 ± 1			
Potentilla fruticosa						<1		
Populus tremuloides	9 ± 9	1 ± 1				<1		
Rosa woodsii	21 ± 13	3 ± 3	6 ± 5	3 ± 2	4 ± 3	2 ± 1	<1	<1
Rubus idaeus	82 ± 11	84 ± 55	<1					
Shepherdia canadensis	<1	23 ± 23	81 ± 52		26 ± 26			
Symphoricarpos spp.	14 ± 14	5 ± 2	3 ± 2	7 ± 6	5 ± 2	1 ± 1	2 ± 1	2 ± 1
Total	821 ± 220^{ab}	1019 ± 291^a	1220 ± 265^a	948 ± 279^{ab}	550 ± 161^{ab}	681 ± 155^{ab}	426 ± 143^{ab}	100 ± 94^b
GRAND TOTAL	1931 ± 132^a	1523 ± 252^{ab}	1456 ± 306^{ab}	1226 ± 306^{ab}	720 ± 129^{bc}	756 ± 127^{bc}	485 ± 133^b	113 ± 96^c

TABLE 6. Understory production (kg ha^{-1}, oven-dried basis) for 1981 in pole-sized ponderosa pine stands growing at different tree stocking levels, Black Hills, South Dakota. Numbers are means ± standard errors. Values within a row followed by different letters are significantly different at the 0.10 probability level.

		Growing stock levels (m^2 ha^{-1})			
	Clearcuts	5	14	23	Unthinned
GRAMINOIDS					
Agropyron caninum	41 ± 9	26 ± 3	<1	<1	
Aristida purpurea				<1	
Bromus porteri		2 ± 2			
Carex spp.	83 ± 26^{a}	60 ± 23^{a}	7 ± 5^{bc}	14 ± 4^{b}	<1 ± <1^{c}
Danthonia intermedia	651 ± 95	365 ± 60	95 ± 17	30 ± 15	<1
Festuca ovina	17 ± 8	<1	3 ± 3		
Koeleria pyramidata	10 ± 10	4 ± 2	<1		
Oryzopsis asperifolia	11 ± 8	24 ± 13	7 ± 3	15 ± 15	
Oryzopsis pungens	5 ± 5			2 ± 2	
Phleum pratense	1 ± 1				
Poa pratensis	89 ± 37	<1			
Poa interior	5 ± 1	1 ± <1	<1		
Unknown grass	2 ± 2	<1	<1	<1	
Total	916 ± 81^{a}	484 ± 63^{b}	113 ± 26^{c}	61 ± 30^{cd}	4 ± 3^{d}
FORBS					
Achillea millefolium	72 ± 18	15 ± 3	5 ± 3	<1	<1
Agoseris glauca	5 ± 4	<1			
Antennaria neglecta	23 ± 15	7 ± 7	3 ± 3	3 ± 1	1 ± <1
Apocynum androsaemifolium	1 ± <1	5 ± 4	2 ± 2	<1	<1
Astragalus spp.	17 ± 9	2 ± 1	1 ± 1	<1	
Astragalus adsurgens	4 ± 2	21 ± 10	25 ± 13	5 ± 4	
Astragalus canadensis	17 ± 14	34 ± 28	9 ± 9	<1	
Astragalus tenellus	5 ± 3	7 ± 6	5 ± 5	13 ± 6	
Campanula rotundifolia	39 ± 8	5 ± 2	2 ± 2		<1
Cirsium vulgare	1 ± 1				
Delphinium bicolor		<1			
Erigeron subrinervis	10 ± 9	<1	<1	<1	
Fragaria vesca	12 ± 7	7 ± 2	1 ± <1	<1	<1

Rubus idaeus produced more at the 3 lower sapling GSLs in 1976 (Table 2), while *Arctostaphylos uva-ursi* was more abundant in pole clearcuts in 1981 (Table 6). Pase (1958) noted the same patterns of *Arctostaphylos uva-ursi* abundance, but this species did not occur in Wrage's (1994) study area. *Symphoricarpos occidentalis* was the most common shrub noted by Wrage (1994) under all *Pinus* canopy levels. *Juniperus communis* (common juniper), rare on our study site and on Wrage's (1994), was abundant on sites studied by Pase (1958). This species is a predominant constituent of *Pinus ponderosa* understory on limestone-derived soils (Thilenius 1972, Hoffman and Alexander 1987).

Fourteen shrub species occurred under the *Pinus* canopy, 11 of which were common to both sapling and pole-sized stands. One species, *Vaccinium scoparium* (grouseberry), was unique to sapling stands and was common in higher GSLs (Tables 1–3). None of the shrub species under saplings were categorized as uncommon. Three species, all unique to pole-sized stands, were classed as uncommon: *Juniperus communis*, *Betula paperifera* (paper birch), and *Potentilla fruticosa* (shrubby cinquefoil). Pase (1958) counted 18 shrub species, while Wrage (1994) noted only 6.

There were no differences ($P < 0.05$) in number of shrub species among sapling GSLs; they ranged from 6 to 8 across all levels with no apparent pattern. In pole stands 8 shrub species occurred in clearcuts but only 4 species were found in GSL 5 (Uresk and Severson 1989). Wrage (1994) did not note any differences. He found 4 shrub species under open, 5 under intermediate, and 5 under dense *Pinus* canopies. None of the shrubs found in the understory of our study or Wrage's were exotic.

TABLE 6. Continued.

		Growing stock levels (m^2 ha^{-1})			
	Clearcuts	5	14	23	Unthinned
Galium boreale		<1	<1	<1	
Hedysarum alpinum					<1
Iris missouriensis	1 ± 1				
Lathyrus ochroleucus	57 ± 27	48 ± 15	34 ± 13	21 ± 11	2 ± 2
Linaria vulgaris	1 ± 1				
Monarda fistulosa		<1			
Polygonum persicaria	<1				
Rumex acetosella	<1				
Solidago sparsiflora	2 ± 1	4 ± 2	5 ± 2	<1	
Taraxacum officinale	2 ± 4	<1			
Trifolium repens	91 ± 33	15 ± 12			
Vicia americana	2 ± 2	5 ± 5	7 ± 6	3 ± 2	<1
Viola adunca	19 ± 6	12 ± 5	<1	<1	<1
Total	385 ± 11^{a}	189 ± 12^{b}	100 ± 8^{c}	44 ± 15^{d}	6 ± 3^{d}
SHRUBS					
Amelanchier alnifolia	1 ± 1	<1	3 ± 2		
Arctostaphylos uva-ursi	1110 ± 102^{a}	864 ± 144^{ab}	673 ± 115^{b}	522 ± 91^{b}	26 ± 18^{c}
Berberis repens		34 ± 34			<1
Juniperus communis				<1	
Populus tremuloides	93 ± 93	<1			
Prunus virginiana	1 ± 1				
Rosa woodsii	22 ± 84	2 ± 2	6 ± 3	<1	2 ± 2
Rubus idaeus	96 ± 56	36 ± 12			
Shepherdia canadensis			215 ± 148	7 ± 7	
Spiraea betulifolia	5 ± <1	3 ± <1	6 ± 1	2 ± <1	1 ± <1
Symphoricarpos spp.	16 ± 11	4 ± 1	8 ± 5	3 ± 2	3 ± 1
Total	1344 ± 43^{a}	945 ± 116^{ab}	910 ± 144^{ab}	535 ± 97^{b}	31 ± 19^{c}
GRAND TOTAL	2644 ± 35^{a}	1620 ± 86^{b}	1123 ± 132^{b}	640 ± 112^{c}	41 ± 21^{d}

Total Understory Response

Total understory production was variable among GSLs; but, generally, the greatest amounts in sapling stands were produced at GSL 23 m^2 ha^{-1} or less and in pole stands at GSL 14 m^2 ha^{-1} or less. Unthinned stands consistently produced significantly less forage than all other GSLs (Tables 1–6). The same trend was noted by Pase (1958).

We identified 89 species in the *Pinus ponderosa* understory over all stocking levels and tree size classes. An additional 19 plants were identified only to genus, and 6 others were designated as unknowns. Pase (1958), who sampled a greater variety of sites, found a total of 119, while Wrage (1994) tallied 70. Hoffman and Alexander (1987) sampled 10 stands in the *Pinus ponderosa/Arctostaphylos uva-ursi* habitat type and found the range of the total number of species to be 13–29. Uresk and Severson (1989) found more species ($P < 0.05$) in sapling and pole clearcuts (34 and 40, respectively) than in mid-level GSLs (saplings 27–28, poles 22–24). Fewest species were found in unthinned stands (23 in sapling and 12 in pole stands). The only species occurring regularly in unthinned stands were *Oryzopsis asperfolia, Danthonia intermedia, Lathyrus ochroleucus,* and *Arctostaphylos uva-ursi* (Tables 1–6).

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Pinus ponderosa is the most abundant and widely distributed tree in the Black Hills. It is the major climax tree species in 7 of 12 forested habitat types described by Hoffman and Alexander (1987) and a seral or occasional species in 2 others. The climax stands occupy about 600,000 ha (Boldt et al. 1983). Natural regeneration of *Pinus ponderosa* in the Black Hills is aggressive and prompt, with high stand densities often resulting (Boldt and Van Duesen 1974, Hoffman and Alexander 1987). Therefore, *Pinus ponderosa* often replaces itself when the stand is disturbed. Only 2 of 7 *Pinus ponderosa* habitat types have potential seral stages dominated by *Populus tremuloides. Quercus macrocarpa* (bur oak) is a minor seral species on another (Hoffman and Alexander 1987). Evidence indicates that eliminating or reducing the *Pinus ponderosa* overstory will increase the number and total productivity of understory species. This has 2 apparent advantages.

First, and most obvious, is that such a reduction is a viable approach to increasing plant species richness of the Black Hills. The habitat type we studied, *Pinus ponderosa/Arctostaphylos uva-ursi*, is not the most floristically rich. We could expect even more dramatic responses to occur in those habitat types that have more species (e.g., *Pinus ponderosa/Quercus macrocarpa* habitat type; Hoffman and Alexander 1987: Table 4). Hence, each *Pinus*-dominated habitat type would likely have a unique understory response to canopy changes. Eliminating *Pinus* overstory in those habitat types where seral stages are dominated by aspen would create an even more diverse community structure. Peripheral evidence suggests that aspen-dominated stands contain more species than *Pinus* or mixed *Populus tremuloides–Pinus ponderosa* (aspen-pine) stands (Kranz and Linder 1973).

Second, a floristically rich and productive understory would support a healthier population of herbivores. Ruminants can select nutritious diets from a diverse array of plant species (Provenza 1995). *Odocoileus virginianus* (white-tailed deer), for example, have the ability to select a variety of forages that collectively balance nutritional needs (Vangilder et al. 1982). Reducing the number of plant species and the resulting decline in selective feeding ability would also increase competitive interactions among herbivores.

Several exotic species occur in the *Pinus* understory. Some, such as *Taraxacum officinale* and *Trifolium repens*, are ubiquitous within natural systems. Others, like *Cirsium vulgare*, *C. arvense*, and *Convolvulus arvense*, are designated noxious weeds and must be controlled by law. Although they may be locally common, their distribution within *Pinus*-dominated communities is limited. Other exotic species appear to be uncommon and restricted to disturbed sites in open areas, such as skid areas on clearcuts. The presence and distribution of exotic species should be a part of monitoring activities.

A similar status is afforded threatened, endangered, and sensitive plant species in the *Pinus ponderosa* understory. None of the species found in this study or Wrage's (1994) is listed as sensitive in the Black Hills (Fertig 1993). Most listed species are found in mesic habitats, but this should not preclude a more intensive survey of *Pinus* understory.

Most evidence provided herein represents a case for maintaining *Pinus ponderosa* stands at a range of stocking levels. While floristic species richness is greater on clearcuts than in unthinned stands, the total number of plant species would be greater if both clearcut and unthinned stands were present. Species such as *Linnaea borealis* (twinflower), *Shepherdia canadensis* (buffaloberry), and *Vaccinium scoparium* (grouseberry) are more common under relatively dense *Pinus* canopies. From an economic standpoint, clearcuts and very low *Pinus* stocking levels promote more growth of available forage for livestock, while intermediate stocking levels produce more wood fiber (Severson and Boldt 1977). Wild ungulates need open areas for foraging and dense conifer stands for cover; intermediate stocking levels provide only marginal levels of both (Sieg and Severson 1996).

Historical evidence shows that patterns of biotic community development in the Black Hills prior to Euro-American intervention were more heterogeneous than those found today, primarily due to the influence of fire (Graves 1899, Progulske 1974, Turchen and McLaird 1975; see also USDA Forest Service 1994, Sieg and Severson 1996), although a few large, dense *Pinus* stands did exist (Graves 1899). We examined only influences of mechanical tree removal; the inclusion of prescribed fire would have produced different results (Sieg and Severson 1996). Litter removal by burning would stimulate a faster understory response (due to exposure of mineral soil and rapid nutrient release). A different species response in the understory could also be expected. For example, nonsprouting species would be less abundant and sprouting species relatively more abundant. Other species, such as *Epilobium* *angustifolium* (fireweed), characteristically invade burned sites (Great Plains Flora Association 1986).

A serious approach to ecosystem management, including concern for health and maintenance of natural systems and economic and social needs, should consider all habitat types and all seral stages within those habitat types. Special attention must be given to placing these in optimum spatial and temporal mosaics. Such mosaics would include the presence of relatively large, dense *Pinus* stands which were present in the Black Hills prior to this century (Graves 1899). The historical pattern of fire-induced community development, coupled with patterns of species responses to overstory reduction, indicates that planning for a higher level of landscape diversity would be a logical approach for ecosystem management in the Black Hills. However, specific goals, under current social and economic constraints, would likely dictate a landscape that differs from one shaped entirely by natural forces.

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BIRD USE OF RIPARIAN VEGETATION ALONG THE TRUCKEE RIVER, CALIFORNIA AND NEVADA

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ABSTRACT.—The Truckee River in California and Nevada is subject to diverse water regimes and a corresponding variety of flow rates. Original riparian vegetation has been altered by these variable flow rates and by a variety of human uses resulting in loss of native riparian vegetation from its historic extent. We conducted bird surveys along the Truckee River during spring 1993 to (1) determine relationships between birds and the present vegetation; (2) determine the importance of different vegetation types to sensitive bird species that have declined recently in the western United States due to competition from exotic plant species, cowbird (*Molothrus ater*) parasitism, reduction in nesting habitat, or other unidentified reasons; and (3) establish a monitoring program and collect baseline data for future comparisons. The most frequently detected bird species throughout the study was the Brown-headed Cowbird. The greatest number of bird species (98 of 116) was found in the native mixed willow (*Salix* spp.) riparian scrub vegetation type. We recommend protecting the remaining native riparian vegetation types for bird habitat along the Truckee River.

Key words: bird abundance, bird species richness, riparian habitat, Truckee River, vegetation type.

Numbers of Neotropical migratory birds are declining throughout North America (Martin and Finch 1996). Explanations for this decline include reduction and fragmentation of breeding, wintering, and migratory stopover habitat (Stevens et al. 1977, Finch 1991a). Riparian corridors are well-known breeding and migratory stopover sites for many Neotropical migrants (Bottorff 1974, Stevens et al. 1977, Wauer 1977, Szaro and Jakle 1985). These corridors are important as cover and foraging habitat for birds migrating through sparsely vegetated desert areas (Sprunt 1975, Stevens et al. 1977). Historically, such corridors existed along the Truckee River and its tributaries in northeast California and northwest Nevada (Ridgway 1877, Klebenow and Oakleaf 1984).

At present the native riparian vegetation along the Truckee River is greatly reduced from its historical extent (Klebenow and Oakleaf 1984, USFWS 1993). A number of factors have contributed, and continue to contribute, to the reduction in riparian vegetation since the late 1800s, including varied flow rates from diversions of water for agricultural use, channelization of parts of the river in the early 1960s, logging, gravel removal, and grazing (Klebenow and Oakleaf 1984). Consequently, the Truckee River riparian corridor is now a thin, discontinuous ribbon of cottonwoods (*Populus* spp.) and willows (*Salix* spp.; USFWS 1993) ranging up to 250 m wide, but averaging approximately 30–50 m wide where present.

Currently, there are no baseline data relating bird populations to vegetative communities along the Truckee River. Our study was designed in cooperation with the U.S. Fish and Wildlife Service (USFWS) to establish a systematic sampling scheme for monitoring bird numbers and species composition along the Truckee River, and to obtain quantitative baseline data on bird-vegetation relationships to satisfy the USFWS operating plan for the Truckee River. Our specific objectives were to determine (1) bird species composition and relative abundances of birds in the major vegetation types, (2) bird species most likely to be impacted by alterations of the native riparian plant communities, and (3) vegetative components (successional stage and species composition) that contribute most to bird abundance and species richness.

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STUDY AREAS

We conducted our study along the Truckee River, California and Nevada (approximately 80 km), and the Little Truckee River (16 km) and Independence Creek (3.5 km), California (Fig. 1). We divided the Truckee River into "lower" (Pyramid Lake to Sparks, Nevada) and "upper" (Floriston, Nevada, to Lake Tahoe) sections based on the approximate elevational border where Fremont cottonwood (*Populus fremontii*) changes to higher-elevation black cottonwood (*P. trichocarpa*; USFWS 1993).

Vegetation along the lower Truckee River is characterized by a narrow but extensive strip of willow (*Salix* spp.), intermixed with occasional clumps of variously aged Fremont cottonwoods. Agricultural development, wide-

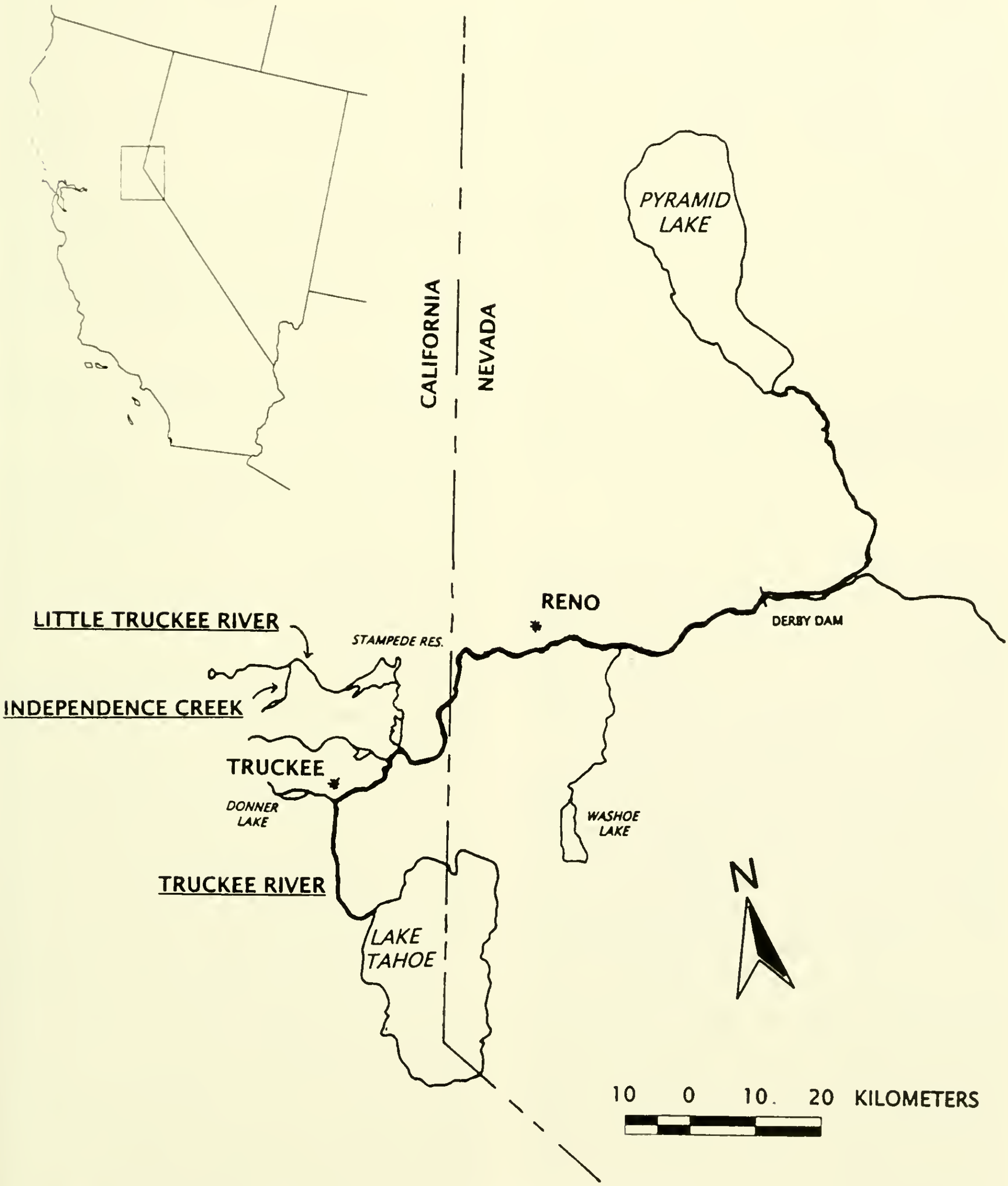
PYRAMID LAKE
CALIFORNIA
NEVADA
RENO
DERBY DAM
LITTLE TRUCKEE RIVER
STAMPEDE RES.
INDEPENDENCE CREEK
TRUCKEE
DONNER LAKE
WASHOE LAKE
TRUCKEE RIVER
LAKE TAHOE
N
10 0 10 20 KILOMETERS

Fig. 1. Map of study site: Truckee River, California and Nevada; and Little Truckee River and Independence Creek, California.

spread along most sections of the lower Truckee, is especially prevalent near the confluence of the Truckee River with Pyramid Lake Reservoir; cattle grazing also is common near this confluence. Hillsides bordering the riparian corridor are dominated by upland shrubs (primarily shadscale [*Atriplex confertifolia*] and black greasewood [*Sarcobatus vermiculatus*]). Exotic whitetop (or peppergrass [*Cardaria draba*]) dominates open, disturbed sites.

Vegetation along the upper Truckee River is also characterized by a narrow strip of willow-cottonwood association. Black cottonwood replaces Fremont cottonwood between 1800 and 2150 m elevation. Uplands are dominated by big sagebrush (*Artemisia tridentata*). Riparian vegetation, and especially black cottonwoods, becomes less dense with increasing elevation. Extensive stands of mixed conifer forest reach the riverbanks and dominate the vegetation at higher elevations (1800–2750 m). Vegetation along the Little Truckee and Independence Creek resembles the upper Truckee River, except the riparian zones along the 2 smaller rivers are dominated by willow-alder (*Alnus tenuifolia*) and riparian scrub, characterized by willow thickets (Appendix).

METHODS

We conducted a preliminary study during the fall of 1992 to locate appropriate study areas and determine the latter extent of the breeding season of locally breeding birds. Observers walked various stretches of the Truckee River and recorded the presence and frequencies of bird species encountered.

During April–July 1993 we sampled birds using the variable circular-plot method (Ralph et al. 1993, Murray and Stauffer 1995). We established evenly spaced points along transects (Reynolds et al. 1980) which were distributed systematically along the Truckee River in a manner that roughly corresponds to the river stretches used by the USFWS for vegetation typing (USFWS 1993). Vegetation types were identified and quantified by measurements of percent cover on 1992 aerial photographs (Appendix, Table 1; USFWS 1993). Vegetation maps were verified by field observations; vegetation types were homogeneous and well defined.

Within each river stretch we placed transects in vegetation types roughly proportional to their occurrence, ensuring adequate representation of the patchy, scattered willow and cottonwood vegetation types. Because the riparian vegetation is patchy and thin, most survey points sampled >1 vegetation type. Transects were also distributed along Little Truckee River and Independence Creek. Although transects on Little Truckee and Independence Creek were established to bisect riparian vegetation, aerial photos were not available for these streams and so vegetation was not quantified.

The beginning of each transect was randomly determined. We established fixed points 200 m apart along each transect, which ran parallel to, and within 10 m of, the stream and within or adjacent to the riparian corridor. Channelization of the river determined that the transects would be linear, ensuring that points were ≥200 m apart. Although the number of points varied among transects due to differences in the extent of riparian vegetation and accessibility of riverbank, all transects had at least 8 points. We surveyed a total of 250 points as follows: lower Truckee, 136; upper Truckee, 51; Little Truckee, 45; and Independence Creek, 18.

We surveyed along the lower Truckee first because the breeding season began earlier there relative to the other areas (M.L. Morrison, unpublished field notes, 1992). While this may have confounded our results because we included migrants, only 5 species that we detected were not common breeders in the area (Ring-billed Gull, California Gull, Black-chinned Hummingbird, Yellow-breasted Chat, and Blue Grosbeak; scientific names in Table 2). These species were all detected in appropriate breeding habitat and may have been residents, but they were rarely detected and had little impact on our conclusions. In addition, all of these species except Ring-billed Gull have bred in this area historically (Ridgway 1877) and therefore were potential breeders during our study.

All points were sampled 3 times, with each transect surveyed forward twice and backward once. We completed a round of surveys on each transect before beginning a new round. Surveys in the lower Truckee were conducted from mid-April to June by 2 observers, and in the other areas from June to early July by 2 different observers. With the exception of one 15-point transect counted by the same observer all 3 times, each transect was surveyed by 2

TABLE 1. Percent cover of major vegetation types along the lower, upper, and overall Truckee River, and number of birds observed, expected, and the difference (from χ^2 analysis), Truckee River, California and Nevada (USFWS 1993).

	Percent cover			Number of birds[a]		
Vegetation type	Lower	Upper	Overall	Observed	Expected	Difference
Open water						
Riverine	12	25	18	—[b]	—	—
Ponds	1	<1	<1	—	—	—
Forest						
Sierra mixed conifer[c]	0	3	2	636	391	–230
Black cottonwood[d]	0	7	4	219	521	–302
Fremont cottonwood–willow[e]	8	3	6	2018	782	+1236
Shrub						
Alder-willow	0	12	6	43	782	–739
Riparian scrub–mixed willow[f]	12	7	10	3011	1303	+1708
Marsh	3	3	3	161	391	–230
Gravel bars	10	3	7	56	912	–856
Sage steppe	16	6	10	1033	1303	–270
Whitetop (peppergrass)	14	6	10	381	1303	–922
Agriculture	23	14	18	—	—	—

[a] Based on 7558 observations, does not include Little Truckee River or Independence Creek observations.

[b] Not quantified for these vegetation types/areas.

[c] Includes lodgepole pine, Jeffrey pine, and mixed conifer forest.

[d] Includes seedling, pole-sapling, and mature stages of black cottonwood.

[e] Includes seedling, pole-sapling, and mature Fremont cottonwood, with and without whitetop.

[f] Includes riparian scrub with and without whitetop.

different observers over the season to standardize observer bias (Verner 1985). All observers were trained by 1 technician and tested against each other to minimize inter-observer bias. Before performing a count, each crew member was tested on a practice count where at least 90% of all detections were identical between trainer and trainee. Species identification and distance estimations were checked across observers by informal testing throughout the sampling season. The paces of each observer were measured by walking 50 m for 3 replications at normal speed. Distance estimations were checked by pacing to stationary objects throughout the season (Ralph et al. 1993).

We counted birds at each point for 5 min. All counts were conducted within the first 4 h after sunrise and only on days without precipitation or significant wind. Before beginning a count, the observer waited for 1 min to allow possibly disturbed birds to resume their normal behaviors (Murray and Stauffer 1995). All birds seen or heard at each point were recorded. We also recorded the vegetation type in which each bird was located (Appendix), detection mode (visual, song, call), and distance from the point to the bird. Before beginning any survey, each observer was shown examples of all vegetation types, which were distinct and easily identifiable. Therefore, we could locate the birds precisely and accurately enough to confidently associate them with vegetation types when the vegetation could be seen. When it could not be seen during a count, observers sought out and identified the vegetation after the 5-min count.

We analyzed our data to obtain an index of abundance (mean number of birds/point/count; Raphael 1987) and frequency of occurrence (percentage of points at which a species was detected; Verner 1985) for each species discussed. Because we had small sample sizes of individual species in each vegetation type, and distances to birds are often difficult to estimate (Verner 1985), we included all detections, regardless of distance from observer, in our abundance analysis (Blondel et al. 1981, Sliwa and Sherry 1992). We also analyzed our data to obtain distribution of birds by vegetation type, highlighting bird species richness within vegetation types and distribution of species among vegetation types.

To test the validity of comparing bird detections among vegetation types, we examined the relationship among major vegetation types and the distribution of detections of birds by distance from the point center using chi-square analysis. This analysis tested whether detectability (measured by average detection distance) of bird species varied among vegetation types. Had they differed, comparisons of bird abundance between vegetation types would have

TABLE 2. Index of abundance[a] ($\bar{x}$) and frequency of occurrence[b] (%) of birds along the lower Truckee, upper Truckee, and Little Truckee rivers and Independence Creek, Nevada and California, spring 1993. Species of special interest are identified with superscripts[c].

Species (Scientific name[h])	Lower Truckee[d]			Upper Truckee[e]			Little Truckee[f]			Independence Creek[g]		
	$\bar{x}$	s	%	$\bar{x}$	s	%	$\bar{x}$	s	%	$\bar{x}$	s	%
American White Pelican (*Pelecanus erythrorhynchos*)	8.3	5.7	3	—[i]	—	—	—	—	—	—	—	—
Double-crested Cormorant (*Phalacrocorax auritus*)	0.4	0.1	5	—	—	—	—	—	—	—	—	—
Great Blue Heron (*Ardea herodias*)	0.4	0.1	2	—	—	—	0.3	0.0	1	—	—	—
Snowy Egret (*Egretta thula*)	0.5	0.3	2	—	—	—	—	—	—	—	—	—
Black-crowned Night-Heron (*Nycticorax nycticorax*)	0.3	0.0	1	—	—	—	—	—	—	—	—	—
White-faced Ibis (*Plegadis chihi*)	1.7	0.0	1	—	—	—	—	—	—	—	—	—
Canada Goose (*Branta canadensis*)	2.5	3.3	15	1.7	0.0	1	0.3	0.0	2	—	—	—
Wood Duck (*Aix sponsa*)	0.6	0.3	6	—	—	—	—	—	—	—	—	—
Mallard (*Anas platyrhynchos*)	0.9	0.5	22	1.4	2.0	3	0.3	0.0	1	—	—	—
Northern Pintail (*Anas acuta*)	—	—	—	0.3	0.0	1	—	—	—	—	—	—
Cinnamon Teal (*Anas cyanoptera*)	0.7	0.3	3	—	—	—	—	—	—	—	—	—
Gadwall (*Anas strepera*)	0.7	0.3	2	—	—	—	—	—	—	—	—	—
Unknown duck	0.9	0.8	5	—	—	—	—	—	—	—	—	—
Common Merganser (*Mergus merganser*)	0.8	0.4	6	0.4	0.2	8	1.2	1.3	10	0.3	0.0	2
Turkey Vulture (*Cathartes aura*)	4.2	7.6	2	—	—	—	1.1	0.7	2	—	—	—
Osprey (*Pandion haliaetus*)	0.3	0.0	1	—	—	—	0.3	0.0	1	0.3	0.0	2
Red-tailed Hawk (*Buteo jamaicensis*)	0.4	0.2	7	—	—	—	0.4	0.2	3	—	—	—
Golden Eagle (*Aguila chrysaetos*)	0.3	0.0	1	—	—	—	—	—	—	—	—	—
American Kestrel (*Falco sparverius*)	0.5	0.2	10	—	—	—	—	—	—	—	—	—
California Quail (*Callipepla californica*)	0.6	0.3	16	—	—	—	1.4	1.2	6	—	—	—
American Coot (*Fulica americana*)	0.7	0.6	3	—	—	—	—	—	—	—	—	—
Killdeer (*Charadrius vociferus*)	0.6	0.3	15	—	—	—	0.3	0.0	1	—	—	—
American Avocet (*Recurvirostra americana*)	1.8	1.2	1	—	—	—	—	—	—	—	—	—
Spotted Sandpiper (*Actitis macularia*)	0.4	0.2	9	0.8	0.6	20	0.6	0.3	21	0.3	0.0	2
Long-billed Curlew (*Numenius americanus*)	0.3	0.0	1	—	—	—	—	—	—	—	—	—
Common Snipe (*Gallinago gallinago*)	0.3	0.0	1	—	—	—	—	—	—	—	—	—
Ring-billed Gull (*Larus delawarensis*)	2.1	2.6	1	—	—	—	—	—	—	—	—	—

TABLE 2. Continued.

Species (Scientific name[h])	Lower Truckee[d]			Upper Truckee[e]			Little Truckee[f]			Independence Creek[g]		
	$\bar{x}$	s	%	$\bar{x}$	s	%	$\bar{x}$	s	%	$\bar{x}$	s	%
California Gull[NH] (*Larus californicus*)	0.7	0.5	1	—	—	—	—	—	—	—	—	—
Unknown gull	4.1	6.8	12	—	—	—	—	—	—	—	—	—
Rock Dove (*Columba livia*)	1.2	1.3	4	0.4	0.2	3	—	—	—	—	—	—
Band-tailed Pigeon (*Columba fasciata*)	—	—	—	0.3	0.0	1	—	—	—	—	—	—
Mourning Dove (*Zenaida macroura*)	0.7	0.4	19	0.7	0.0	1	0.3	0.0	1	—	—	—
Great Horned Owl (*Bubo virginianus*)	0.5	0.2	1	—	—	—	—	—	—	—	—	—
Black-chinned Hummingbird (*Archilochus alexandri*)	0.7	0.0	1	—	—	—	—	—	—	—	—	—
Calliope Hummingbird (*Stellula calliope*)	—	—	—	—	—	—	0.6	0.4	2	0.5	0.2	4
Belted Kingfisher (*Ceryle alcyon*)	0.4	0.2	3	0.4	0.2	2	0.3	0.0	2	—	—	—
Red-breasted Sapsucker (*Sphyrapicus ruber*)	—	—	—	0.3	0.0	1	0.5	0.3	4	0.4	0.2	8
Williamson's Sapsucker (*Sphyrapicus thyroideus*)	—	—	—	—	—	—	0.5	0.2	2	0.3	0.0	2
Downy Woodpecker (*Picoides pubescens*)	0.5	0.2	3	0.4	0.2	3	0.3	0.0	1	—	—	—
Hairy Woodpecker[NH] (*Picoides villosus*)	—	—	—	0.3	0.0	1	0.3	0.0	1	0.6	0.5	8
White-headed Woodpecker (*Picoides albolarvatus*)	—	—	—	0.5	0.2	1	0.3	0.0	1	—	—	—
Black-backed Woodpecker (*Picoides arcticus*)	—	—	—	—	—	—	—	—	—	0.3	0.0	2
Northern Flicker (*Colaptes auratus*)	0.5	0.3	3	0.4	0.1	9	0.5	0.3	12	0.4	0.2	4
Olive-sided Flycatcher[?] (*Contopus borealis*)	0.3	0.0	1	0.4	0.1	7	0.3	0.0	1	0.3	0.4	4
Western Wood-Pewee (*Contopus sordidulus*)	0.5	0.3	8	1.2	0.7	23	1.3	0.5	31	1.5	1.0	36
Willow Flycatcher[CB] (*Empidonax trailii*)	—	—	—	0.3	0.0	1	—	—	—	—	—	—
Hammond's Flycatcher (*Empidonax hammondii*)	0.3	0.1	1	—	—	—	—	—	—	—	—	—
Dusky Flycatcher (*Empidonax oberholseri*)	0.3	0.1	2	—	—	—	0.5	0.2	1	0.8	0.4	32
Empidonax species	0.4	0.2	3	0.3	0.5	3	0.5	0.3	10	0.6	0.2	28
Say's Phoebe (*Sayornis saya*)	0.3	0.1	1	—	—	—	—	—	—	—	—	—
Western Kingbird (*Tyrannus verticalis*)	0.7	0.5	18	—	—	—	—	—	—	—	—	—
Tree Swallow[NH,CB] (*Tachycineta bicolor*)	0.4	0.2	1	1.1	1.0	6	—	—	—	0.3	0.0	2
Violet-Green Swallow[NH,CB] (*Tachycineta thalassina*)	0.3	0.0	1	—	—	—	0.3	0.0	1	—	—	—
Northern Rough-winged Swallow (*Stelgidopteryx serripennis*)	0.9	0.9	22	—	—	—	4.3	2.6	5	—	—	—
Bank Swallow[NH] (*Riparia riparia*)	0.8	0.5	5	—	—	—	—	—	—	—	—	—

TABLE 2. Continued.

Species	Lower Truckee[d]			Upper Truckee[e]			Little Truckee[f]			Independence Creek[g]		
(Scientific name[h])	$\bar{x}$	s	%	$\bar{x}$	s	%	$\bar{x}$	s	%	$\bar{x}$	s	%
Cliff Swallow (*Hirundo pyrrhonota*)	1.8	3.3	7	4.1	5.6	6	6.2	7.9	5	—	—	—
Barn Swallow (*Hirundo rustica*)	0.9	0.8	14	1.7	1.7	2	—	—	—	—	—	—
Unknown swallow	0.7	0.7	4	—	—	—	—	—	—	—	—	—
Steller's Jay (*Cyanocitta stelleri*)	—	—	—	1.4	0.8	33	0.8	0.6	22	0.4	0.2	6
Clark's Nutcracker (*Nucifraga columbiana*)	—	—	—	—	—	—	—	—	—	0.7	0.0	2
Black-billed Magpie (*Pica pica*)	1.1	0.9	25	—	—	—	0.7	0.0	1	—	—	—
American Crow (*Corvus brachyrhynchos*)	0.3	0.0	1	—	—	—	—	—	—	—	—	—
Common Raven (*Corvus corax*)	0.3	0.1	2	—	—	—	—	—	—	—	—	—
Mountain Chickadee (*Parus gambeli*)	—	—	—	1.2	0.7	21	0.9	0.7	21	1.2	0.7	36
Bushtit (*Psaltriparus minimus*)	0.5	0.3	1	—	—	—	—	—	—	—	—	—
Red-breasted Nuthatch (*Sitta canadensis*)	—	—	—	0.6	0.3	3	0.3	0.4	2	0.3	0.0	2
White-breasted Nuthatch (*Sitta carolinensis*)	—	—	—	0.5	0.2	1	0.3	0.0	1	0.3	0.0	2
Pygmy Nuthatch (*Sitta pygmaea*)	—	—	—	0.0	0.4	1	—	—	—	—	—	—
Brown Creeper (*Certhia americana*)	—	—	—	0.3	0.4	1	0.4	0.1	5	0.7	0.3	12
Rock Wren (*Salpinctes obsoletus*)	0.4	0.1	5	—	—	—	—	—	—	—	—	—
Bewick's Wren (*Thryomanes bewickii*)	0.8	0.7	14	—	—	—	—	—	—	—	—	—
House Wren (*Troglodytes aedon*)	1.1	0.8	24	1.7	0.9	10	1.6	1.1	4	0.7	0.4	10
Marsh Wren[CB,NH] (*Cistothorus palustris*)	0.3	0.0	1	—	—	—	—	—	—	—	—	—
American Dipper (*Cinclus mexicanus*)	—	—	—	0.3	0.1	3	0.5	0.2	4	—	—	—
Ruby-crowned Kinglet (*Regulus calendula*)	0.3	0.0	1	—	—	—	—	—	—	—	—	—
Blue-Gray Gnatcatcher (*Polioptila caerulea*)	0.3	0.0	1	—	—	—	—	—	—	—	—	—
Mountain Bluebird (*Sialia currucoides*)	—	—	—	—	—	—	0.6	0.4	2	—	—	—
Townsend's Solitaire (*Myadestes townsendi*)	—	—	—	0.3	0.0	1	0.6	0.3	5	—	—	—
Hermit Thrush (*Catharus guttatus*)	—	—	—	—	—	—	—	—	—	0.3	0.0	2
American Robin (*Turdus migratorius*)	0.7	0.5	18	1.0	0.7	29	1.3	0.7	30	1.3	0.9	34
Cedar Waxwing (*Bombycilla cedrorum*)	1.7	0.0	1	—	—	—	—	—	—	—	—	—
European Starling[EX] (*Sturnus vulgaris*)	1.2	1.1	22	0.4	0.2	2	—	—	—	—	—	—
Solitary Vireo (*Vireo solitarius*)	0.4	0.2	1	—	—	—	—	—	—	0.3	0.0	6

TABLE 2. Continued.

Species (Scientific name[h])	Lower Truckee[d]			Upper Truckee[e]			Little Truckee[f]			Independence Creek[g]		
	$\bar{x}$	s	%	$\bar{x}$	s	%	$\bar{x}$	s	%	$\bar{x}$	s	%
Warbling Vireo[CB] (*Vireo gilvus*)	0.4	0.3	6	1.3	0.8	23	1.0	0.6	23	1.9	1.0	36
Orange-crowned Warbler (*Vermivora celata*)	0.3	0.0	1	—	—	—	—	—	—	—	—	—
Nashville Warbler (*Vermivora ruficapilla*)	—	—	—	0.8	0.5	15	0.7	0.0	1	0.3	0.4	4
Yellow Warbler[CB] (*Dendroica petechia*)	0.5	0.4	10	0.9	0.7	21	1.7	1.2	21	1.3	0.9	26
Yellow-rumped Warbler (*Dendroica coronata*)	0.7	0.4	10	0.7	0.4	11	0.7	0.4	14	0.8	0.6	22
MacGillivray's Warbler (*Oporornis tolmiei*)	0.4	0.1	2	0.6	0.2	6	0.4	0.2	3	1.4	0.8	6
Common Yellowthroat[CB] (*Geothlypis trichas*)	0.4	0.1	2	0.3	0.0	1	—	—	—	—	—	—
Wilson's Warbler (*Wilsonia pusilla*)	0.5	0.2	15	0.8	0.6	11	0.7	0.7	9	0.7	0.6	20
Yellow-breasted Chat[CB,NH] (*Icteria virens*)	0.5	0.3	1	—	—	—	—	—	—	—	—	—
Unknown warbler	0.4	0.1	3	—	—	—	—	—	—	—	—	—
Western Tanager[CB] (*Piranga ludoviciana*)	0.4	0.3	3	0.4	0.1	4	—	—	—	—	—	—
Black-headed Grosbeak (*Pheucticus melanocephalus*)	0.5	0.2	6	0.4	0.1	7	0.8	0.8	2	—	—	—
Blue Grosbeak (*Guiraca caerulea*)	0.3	0.0	1	—	—	—	—	—	—	—	—	—
Lazuli Bunting (*Passerina amoena*)	0.5	0.2	7	—	—	—	—	—	—	—	—	—
Green-tailed Towhee (*Pipilo chlorurus*)	—	—	—	0.7	0.5	14	0.7	0.5	8	—	—	—
Spotted Towhee[CB] (*Pipilo maculatus*)	0.7	0.3	1	0.5	0.2	5	—	—	—	—	—	—
Chipping Sparrow[CB] (*Spizella passerina*)	0.3	0.1	2	0.3	0.5	3	0.8	0.5	6	0.4	0.2	8
Brewer's Sparrow (*Spizella breweri*)	—	—	—	—	—	—	0.7	0.4	4	—	—	—
Vesper Sarrow (*Pooecetes gramineus*)	—	—	—	—	—	—	0.6	0.3	4	—	—	—
Black-throated Sparrow (*Amphispiza bilineata*)	0.3	0.0	1	—	—	—	—	—	—	—	—	—
Savannah Sparrow[CB] (*Passerculus sandwichensis*)	0.5	0.2	1	—	—	—	—	—	—	—	—	—
Fox Sparrow (*Passerella iliaca*)	—	—	—	0.5	0.2	8	0.3	0.0	2	—	—	—
Song Sparrow[CB] (*Melospiza melodia*)	0.5	0.3	9	2.1	1.0	33	1.9	1.6	21	1.1	0.8	22
Lincoln's Sparrow (*Melospiza lincolnii*)	—	—	—	0.6	0.4	2	0.6	0.3	3	—	—	—
White-crowned Sparrow (*Zonotrichia leucophrys*)	0.3	0.0	1	—	—	—	0.9	0.7	6	0.3	0.0	6
Dark-eyed Junco (*Junco hyemalis*)	—	—	—	1.1	0.6	17	1.1	0.8	19	1.1	0.7	28
Red-winged Blackbird (*Agelaius phoeniceus*)	1.2	0.9	23	1.7	1.5	5	2.1	1.4	5	—	—	—
Western Meadowlark[CB] (*Sturnella neglecta*)	0.5	0.3	13	—	—	—	—	—	—	—	—	—

TABLE 2. Continued.

Species (Scientific name[h])	Lower Truckee[d]			Upper Truckee[e]			Little Truckee[f]			Independence Creek[g]		
	$\bar{x}$	s	%	$\bar{x}$	s	%	$\bar{x}$	s	%	$\bar{x}$	s	%
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	1.1	1.6	6	—	—	—	—	—	—	—	—	—
Brewer's Blackbird (*Euphagus cyanocephalus*)	1.1	0.9	14	1.4	1.3	13	1.0	0.8	10	—	—	—
Brown-headed Cowbird^{EX} (*Molothrus ater*)	1.5	0.9	32	0.9	0.5	28	0.6	0.4	16	0.5	0.2	22
Unknown blackbird	0.7	0.6	12	—	—	—	—	—	—	—	—	—
Northern Oriole (*Icterus galbula*)	1.0	0.5	28	0.3	0.0	1	—	—	—	—	—	—
Purple Finch (*Carpodacus purpureus*)	—	—	—	—	—	—	0.7	0.7	3	—	—	—
Cassin's Finch (*Carpodacus cassinii*)	—	—	—	0.7	0.0	1	0.9	0.5	4	1.1	0.7	12
House Finch (*Carpodacus mexicanus*)	0.5	0.5	5	—	—	—	—	—	—	—	—	—
Pine Siskin (*Carduelis pinus*)	—	—	—	0.3	0.0	1	0.9	0.2	2	0.8	0.4	6
Lesser Goldfinch (*Carduelis psaltria*)	0.3	0.0	1	—	—	—	—	—	—	—	—	—
House Sparrow^{EX} (*Passer domesticus*)	0.8	0.4	5	—	—	—	—	—	—	—	—	—

[a] Number of birds/point/count.

[b] Number of detections of this species/total # counts on this transect

[c] EX = exotic or opportonistic species, possibly having a negative impact on native species; NH = species with sensitive nesting habitat, impacted by alterations in riparian vegetation; CB = species adversely affected by exotic or opportunistic species; ? = species declining for unknown reason.

[d] 119 points, 357 total counts (points × 3)

[e] 68 points, 204 total counts (points × 3)

[f] 45 points, 135 total counts (points × 3)

[g] 18 points, 54 total counts (points × 3)

[h] AOU 1983, 1995

[i] Not present

been invalid. In a vegetation type where bird calls do not carry well (e.g., dense trees), the average distance of detection will be smaller than in vegetation types where bird calls carry long distances (e.g., open grassland). For 8 of 10 species examined, average detection distance did not vary between vegetation types ($P > 0.1$); the remaining 2 species had $0.05 < P < 0.1$. For these 2 species, average detection distance was shorter in riparian scrub than in other vegetation types. Some of our data, therefore, are slightly, but not usually significantly, biased toward fewer detections in the riparian scrub vegetation type; however, the number of detections in this vegetation type for these species exceeds detections in any other vegetation type. Also, our survey points often sampled multiple vegetation types; therefore, the distance from the point center to a given vegetation type varied. Riparian vegetation tended to be most consistently nearer the point center, thus explaining some of the bias.

We also conducted chi-square analyses to determine if there is a difference between general bird use of vegetation types and availability of these vegetation types to the birds. Because our survey focused on nonagricultural vegetative relationships, for this analysis we excluded individual birds detected in agricultural areas and areas that were not quantified on vegetation maps (36% of all detections).

Throughout this paper we discuss general trends for all bird species, focusing on 21 avian species of special interest (Tables 2, 4). These species include those thought to be decreasing in abundance due to competition from opportunistic and exotic species or thought to be impacted by alterations of riparian vegetation. Other species of interest may be increasing opportunistic and exotic species (e.g., Brown-headed Cowbird, European Starling, House Sparrow) that may adversely impact riparian birds. Identification of these species of special interest was designated by the USFWS based on review of previous works (Ridgway 1877, Klebenow and Oakleaf 1984) and communication with regional biologists (USFWS, California Parks Department).

RESULTS

Species Richness and Abundance of Birds

OVERALL.—We detected 116 species across the entire study area. The most abundant species overall was Cliff Swallow, followed by American White Pelican, Song Sparrow, Turkey Vulture, Northern Rough-winged Swallow, and House Wren (Table 2). Mean ± *s* of bird species richness per point was 16 ± 4 among transects on the lower Truckee, 14 ± 4 on the upper Truckee, 13 ± 2 on the Little Truckee, and 13 ± 4 on the single Independence Creek transect. Total bird abundance on each transect ranged between 8.7 and 14.8 birds/point/count, with a mean of 11.2 ± 1.8 birds/point/count.

LOWER TRUCKEE RIVER.—The most frequently detected bird species along the lower Truckee was the Brown-headed Cowbird, followed by Northern Oriole, Black-billed Magpie, House Wren, Red-winged Blackbird, European Starling, Northern Rough-winged Swallow, and Mallard (Table 2). Eighteen species of special interest were detected along the lower Truckee, 4 at >10% of the counts and the remaining 14 at ≤9% of the counts (Table 2).

UPPER TRUCKEE RIVER.—The most frequently detected species along the upper Truckee was the Song Sparrow, followed by Steller's Jay, American Robin, Brown-headed Cowbird, Warbling Vireo, Western Wood-Pewee, Mountain Chickadee, Yellow Warbler, and Spotted Sandpiper. Twelve species of special interest were detected along the upper Truckee, 4 at >20% of the counts and the remaining 8 at ≤6% of the counts (Table 2).

LITTLE TRUCKEE RIVER.—Along the Little Truckee the most frequently observed bird species was the Western Wood-Pewee, followed by American Robin, Warbling Vireo, Steller's Jay, Mountain Chickadee, Song Sparrow, Spotted Sandpiper, and Yellow Warbler. Seven species of special interest were detected along the little Truckee: 4 were detected at >10% of the counts and 3 at ≤6% (Table 2).

INDEPENDENCE CREEK.—The most frequently detected bird species on Independence Creek was the Mountain Chickadee, followed by Warbling Vireo, Western Wood-Pewee, American Robin, Dusky Flycatcher, Dark-eyed Junco, unidentified *Empidonax* flycatchers, Yellow Warbler, Brown-headed Cowbird, Song Sparrow, Yellow-rumped Warbler, and Wilson's Warbler. Seven species of special interest were detected along Independence Creek: 4 were detected at >20% of the counts and 3 at ≤8% (Table 2).

Over all sections of the river, ≤2 individuals of each of the most frequently detected species were observed during any single point count (Table 2).

Distribution of Birds by Vegetation Type

RICHNESS AND PERCENT OCCURRENCE OF BIRDS AMONG VEGETATION TYPES.—We did not sample each vegetation type equally throughout the Truckee River drainage; therefore, the following 3 results sections should be considered as baseline data to be compared with future avian sampling.

The highest bird species richness occurred in the riparian scrub vegetation type, with 17 species detected only in riparian scrub. Sagebrush steppe, riparian scrub with whitetop, mature Fremont cottonwood with and without whitetop, pole-sapling Fremont cottonwood with and without whitetop, whitetop alone, and Sierra mixed conifer also had high species richness (≥40; Table 3). Of 116 bird species observed during our study, only the Pine Siskin, White-breasted Nuthatch, White-faced Ibis, Blue-Gray Gnatcatcher, Brown Creeper, Black-throated Sparrow, Cedar Waxwing, and Hairy Woodpecker were never detected in native riparian vegetation.

Species richness was 30% less in riparian scrub that contained whitetop. However, bird richness in Fremont cottonwood was the same with and without whitetop (Table 3).

Riparian scrub vegetation had the highest percentage of detections of all species over all points in our study. Sagebrush steppe was the only other vegetation type with >10% of all birds detected. No single successional stage of cottonwood had >8% of all detections; however, 21.2% of all birds observed were across

TABLE 3. Species richness (number) and percentage of all birds detected (%) by vegetation type, Truckee River and vicinity, California and Nevada, spring 1993.[a]

Vegetation type[b]	Number	%
Pole-sapling Fremont cottonwood–willow	49	3.3
Mature Fremont cottonwood–willow	53	6.6
Seedling Fremont cottonwood–willow with whitetop	9	0.1
Pole-sapling Fremont cottonwood–willow with whitetop	48	3.7
Mature Fremont cottonwood–willow with whitetop	57	7.5
Riparian scrub	93	28.7
Riparian scrub with whitetop	62	9.6
Whitetop	49	4.3
Sage steppe	77	14.0
Marsh	27	1.6
Gravel bar	17	0.5
Seedling black cottonwood	5	0.1
Pole-sapling black cottonwood	18	0.8
Mature black cottonwood	28	1.5
Jeffrey pine	39	4.1
Lodgepole pine	40	5.8
Sierra mixed conifer	42	5.7
Agriculture	34	2.1

[a]Based on 11,812 observations.

[b]See Appendix for full description of vegetation types.

all stages of Fremont cottonwood. Pure whitetop stands supplied 4.3% of all detections (Table 3).

The percentage of individual birds detected was low in all conifer vegetation types (<6%). Overall, the 3 conifer vegetation types—Jeffrey pine (*Pinus jeffreyi*), lodgepole pine (*Pinus contorta* var. *murrayana*), and mixed conifer—contained 15.6% of all birds detected. Black cottonwood, which occurs within the conifer zone, contained only 2.4% of bird occurrences (Table 3).

BIRD SPECIES DETECTIONS ACROSS VEGETATION TYPES.—Thirteen species were detected in ≥10 vegetation types, whereas 40 species were detected in ≤3 different types. Brown-headed Cowbirds (Table 4) and American Robins were detected in all vegetation types, and both were most commonly detected in riparian scrub vegetation.

FREQUENCY OF BIRD SPECIES OF SPECIAL INTEREST AMONG VEGETATION TYPES.—We considered a bird species to be rare if it was detected with a frequency of ≤2.5% (during <20 of the 750 total point counts).

EXOTIC OR OPPORTUNISTIC SPECIES.—Brown-headed Cowbirds were common and were detected in all vegetation types, though less frequently at higher elevations (Table 4). European Starlings were frequently detected at lower elevations where there were trees, and also in sagebrush steppe. Similarly, the introduced House Sparrow was most frequently detected in Fremont cottonwood and riparian scrub at low elevations. Both starlings and House Sparrows were detected primarily near buildings and agricultural fields.

SPECIES POSSIBLY AFFECTED BY EXOTIC OR OPPORTUNISTIC SPECIES, UNKNOWN REASONS, OR ALTERATION IN RIPARIAN VEGETATION.—California Gulls, Common Yellowthroats, Spotted Towhees, Tree Swallows, Willow Flycatchers, Marsh Wrens, Chipping Sparrows, Savannah Sparrows, and Yellow-breasted Chats were rare but most often detected in riparian scrub (Table 4). Tree Swallows were also observed nesting in mature black cottonwood. Olive-sided Flycatchers, thought to be declining throughout the West (Robbins et al. 1986, DeSante and George 1994), were most often observed in Sierra mixed conifer and riparian scrub. Western Meadowlarks were fairly frequent across most vegetation types, and Violet-Green Swallows were only rarely detected; both species were detected only at lower elevations. Song Sparrows were common and Western Tanagers were rarely detected; both were seen across most vegetation types. Warbling Vireos were frequent in riparian scrub, lodgepole pine, and black cottonwood. Yellow Warblers were detected across all riparian types, most frequently in riparian scrub.

SPECIES POSSIBLY IMPACTED BY ALTERATION IN RIPARIAN VEGETATION.—Bank Swallows were most frequently detected in Fremont cottonwood and sagebrush steppe (Table 4). Hairy

TABLE 4. Percent detections of species of special interest among vegetation types[a] along the Truckee River and vicinity, California and Nevada.

Species	cw	cw+w[b]	rs	rs+w	w	ss	m	g	bc	jp	lp	smc	a
Exotic/Opportunistic													
European Starling	19	31	22	13	4	12	<1	<1	0	0	0	0	0
Brown-headed Cowbird	13	12	26	13	8	17	2	1	2	1	1	4	<1
House Sparrow	39	10	49	3	0	0	0	0	0	0	0	0	0
Competition with exotics or unidentified reasons													
Olive-sided Flycatcher	0	0	31	8	0	0	0	0	0	8	8	46	0
Willow Flycatcher	0	0	100	0	0	0	0	0	0	0	0	0	0
Tree Swallow[c]	0	0	42	2	2	0	0	4	46	2	2	0	0
Violet-Green Swallow[c]	0	33	0	0	0	67	0	0	0	0	0	0	0
Marsh Wren[c]	0	0	0	67	0	33	0	0	0	0	0	0	0
Warbling Vireo	1	14	32	3	1	1	0	0	17	2	18	12	0
Yellow Warbler	8	17	43	10	2	4	1	0	9	0	3	4	1
Common Yellowthroat	9	18	0	36	9	18	0	0	0	0	0	9	0
Yellow-breasted Chat[c]	0	25	13	50	13	0	0	0	0	0	0	0	0
Western Tanager	15	20	10	15	0	0	5	5	5	5	0	20	0
Spotted Towhee	0	0	47	24	0	6	0	0	12	6	0	6	0
Chipping Sparrow	0	0	40	0	20	20	0	0	0	0	0	20	0
Savannah Sparrow	0	0	67	0	0	33	0	0	0	0	0	0	0
Song Sparrow	5	2	64	1	2	7	<1	0	5	2	2	12	0
Western Meadowlark	28	26	13	19	2	12	0	0	0	0	0	0	0
Impacted by loss of habitat or vegetation alteration													
California Gull	0	0	100	0	0	0	0	0	0	0	0	0	0
Hairy Woodpecker	0	0	0	0	0	0	0	0	0	0	0	100	0
Bank Swallow	48	0	24	8	8	32	0	0	0	0	0	0	0

[a] Vegetation types and codes found in Appendix.

[b] +w = vegetation type mixed with whitetop.

[c] Also affected by loss of habitat or alteration of vegetation.

Woodpeckers were detected only in Sierra mixed conifer. Both species were rare.

USE VERSUS AVAILABILITY OF VEGETATION TYPES.—Overall, birds did not use vegetation types in proportion to their availability ($\chi^2 = 7254$, df = 8, $P < 0.001$). The discrepancy between use and availability was highest in riparian scrub and Fremont cottonwood. Although totaling only 10% cover (Table 1), riparian scrub/mixed willow was used by birds almost 40% of the time during our observations. Bird use of monotypic whitetop was significantly less than expected given its percent cover. The number of bird species using these vegetation types supports our findings of bird preference: Fremont cottonwood, 70 species; riparian scrub/mixed willow, 80 species; and whitetop, 44 species.

DISCUSSION

Overall Distribution and Abundance of Birds

The lower Truckee River harbored the greatest richness of avifauna of any stream section we monitored. This was due primarily to the section's extensive riparian scrub and Fremont cottonwood stands; these vegetation types decreased in area with increasing elevation (USFWS 1993) on the upper stretches of the river. Higher-elevation black cottonwood communities did not replace lower riparian scrub–cottonwood communities in terms of bird species richness. Elevational temperature gradients and arthropod abundances were not examined in this study but may have contributed to levels of species abundance we observed. Black and Fremont cottonwood each occupied similar absolute areas (Table 1); hence, differences in bird richness were unlikely due to an area effect.

Transects at higher elevations were composed of coniferous vegetation with a narrow strip of streamside riparian vegetation; a conifer overstory was often present at streamside. In contrast, transects at lower elevations were predominantly riparian, with a cottonwood overstory and scrub understory. Thus, by virtue of abundance of vegetation types alone, lower-elevation areas should be dominated by riparian-associated bird species, while upper-elevation areas should have fewer riparian-associated bird species. Knopf (1985) and Finch (1991b) also reported different bird communities associated with different elevations.

Species-specific Considerations

The Brown-headed Cowbird was widely distributed but reached its highest numbers at lower elevations where agriculture was prominent (Table 1). These birds typically forage in agricultural areas while sometimes flying long distances to find forested nesting habitat. The Brown-headed Cowbird was the most frequently encountered bird along the lower Truckee and was also found in the greatest number of vegetation types. Yellow Warbler, Warbling Vireo, Common Yellowthroat, Yellow-breasted Chat, and Song Sparrow were also detected during our study and are known to be adversely impacted by cowbird nest parasitism (Friedmann et al. 1977).

European Starlings, common along the lower Truckee, were especially numerous near agricultural fields and buildings; their numbers decreased rapidly with increasing elevation. Therefore, their potential impact on cavity-nesting species may be of primary concern only at lower elevations (Stoner 1939, Jackson and Tate 1974). House Sparrows were rare and were detected primarily around buildings.

Willow Flycatchers, which are declining in the West (DeSante and George 1994, Rothstein and Robinson 1994), were detected at only 1 point on the upper Truckee River and nowhere else. Dates of the sightings (18 and 24 June) suggest the probability of breeding activity (Bent 1942, McCabe and Hovel 1991), but we were unable to confirm this.

Avifauna of Little Truckee River and Independence Creek were dominated by species typical of coniferous forests. However, Warbling Vireos, Song Sparrows, and Yellow Warblers, all riparian-associated species of concern, were also common in both areas throughout the study. In addition, the Wilson's Warbler, another riparian-associated species, was commonly observed on Independence Creek and, to a lesser extent, on the upper Truckee and Little Truckee. Even in these conifer-dominated areas, small patches of riparian vegetation apparently are enough to support these riparian-associated bird species.

Species Richness in Vegetation

Fremont cottonwood and riparian scrub willow were used by a wide variety of birds and with a much greater frequency than their availability. Therefore, a drastic reduction in native riparian forest abundance may have more effect on birds than a reduction in any other plant species along the Truckee River. Habitat specialists (40 species found in ≤3 different habitat types) were observed most frequently in riparian scrub. Even the habitat generalists in our study (Brown-headed Cowbird and American Robin—the bird species found in the greatest number of different vegetation types) were most frequently observed in riparian scrub. Therefore, both dominant riparian vegetation plants—cottonwood and willow (the dominant plant species in riparian scrub)—should be considered in developing management plans for protecting the habitat of Truckee River bird species.

Because 98 of 116 bird species were detected in native riparian vegetation, 22 exclusively, the majority of bird species would be impacted in some way by altering native riparian plant communities. Although sagebrush steppe also had a high species richness, this is probably due to its proximity to riparian vegetation, creating an ecotone that attracts more species than the sagebrush-steppe vegetation type alone (Gates and Gysel 1978).

Impacts of Exotic Vegetation

The major exotic plant of interest in our study was whitetop, or peppergrass. Whitetop was used by bird species for foraging (S. Lynn personal observation), but nesting in this plant species was not documented. Whitetop was negatively associated with bird species richness in riparian scrub; however, bird richness in Fremont cottonwood did not differ with the presence of whitetop. Further research in this area is necessary to determine whether there is a cause-effect relationship between whitetop and bird species richness.

In summary, a varied flow regime, overgrazing, channelization, and other human activities have altered riparian vegetation along the Truckee River and its tributaries (Klebenow and Oakleaf 1984). Destruction and removal of native cottonwoods and willows from the riparian corridor has likely resulted in a decrease in numbers of riparian obligate bird species, a historical issue which will be presented in a future manuscript. Also, avian exotics and opportunistic species, such as the Brown-headed Cowbird, could potentially reduce sensitive species richness and abundance. The effects of cowbird parasitism and exotic species on sensitive bird species in the Truckee River area warrant further investigation. Also warranting further investigation is the effect that the exotic plant species whitetop may have on bird distribution. Unfortunately, whitetop is an especially hardy species that is difficult to eradicate (Rosenfels and Headley 1944). Management plans may have to consider it as a permanent aspect of the riparian community and concentrate on keeping existing patches of the plant from spreading into native riparian habitats.

Managers who are interested in halting declines in bird populations and stimulating growth in these populations should consider protecting existing native Fremont cottonwoods and riparian scrub vegetation, as well as perhaps initiating restoration of these vegetation types in degraded areas. Data that we collected will be valuable as a baseline from which to compare future bird surveys along these rivers as land uses change or continue in degradation of native riparian forest. Future researchers will be able to use our data to discover and confirm trends among bird species and their vegetation requirements along the Truckee River and vicinity.

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APPENDIX. Major vegetation types along the Truckee River, California and Nevada (USFWS 1993).

Code	Vegetation type and characteristics
smc	*Sierra mixed conifer forest:* An open, parklike forest of coniferous evergreens with crowns often touching. Several predominant species: *Abies*, *Pseudotsuga*, and *Cornus* are most common on moist sites; *Pinus* spp. and *Ceanothus* spp. on dry sites. The understory typically is sparse, consisting of scattered chaparral shrubs and young trees. Elevation: 1500–2100 m.
jp	*Jeffrey pine:* A tall, open forest predominated by Jeffrey pine, with sparse understory of montane chaparral or sagebrush spp. Elevation: 2100–2750 m.
lp	*Lodgepole pine:* Typically a dense forest of slender trees up to 40 m tall, often in pure stands. Elevation: 2100–2750 m.
bc	*Black cottonwood:* A fairly dense, mixed riparian forest predominated by black cottonwood with Jeffrey pine and/or lodgepole pine. The shrub and herb layers are well developed. Elevation: usually >1800 m.
cw	*Great Basin cottonwood-willow forest:* Open-canopied forest predominated by Fremont cottonwood and *Salix laevigata* (primarily east of Vista). Elevation: usually <2100 m. This type was further delineated by the presence of whitetop ("/w" added to ending of type code) and by successional stage: cw2 = shrub seedling (<3 m tall); cw3 = pole-sapling; cw4 = mature.
rs	*Great Basin riparian scrub:* Open to dense riparian thickets usually composed of willow. Open stands may have a dense herbaceous understory. Elevation: all, but especially well developed along lower Truckee.

APPENDIX. Continued.

Code	Vegetation type and characteristics
ss	*Sagebrush steppe:* A semiclosed steppe predominated by big sagebrush with several perennial bunchgrasses between shrubs. Elevation: below conifer zone.
m	*Freshwater marsh:* Predominated by perennial, emergent monocots. *Scirpus* and *Typha* dominate. Sites lack current, often permanently flooded freshwater (backwater of Derby Dam, oxbow).
a	*Aspen:* Dense stands of usually mature aspen located within conifer zone.
g	*Gravel bars.*
w	*Whitetop:* Low, dense, exotic forb. Dead stalks persistent and woody. Often is dominant understory for Fremont cottonwood. Elevation: <1800 m.
ag	*Agriculture, mostly alfalfa.*

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USE AND SELECTION OF BROOD-REARING HABITAT BY SAGE GROUSE IN SOUTH CENTRAL WASHINGTON

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ABSTRACT.—Sage Grouse (*Centrocercus urophasianus*) brood-habitat use was examined during 1992 and 1993 at the Yakima Training Center in Yakima and Kittitas counties, Washington. During the 2 yr we followed 38 broods, of which 12 persisted to 1 August ($\bar{x}$ = approximately 1.5 chicks/brood). Food forb cover was greater at all brood locations than at random locations. Hens with broods in big sagebrush/bunchgrass habitat (*Artemisia tridentata/Agropyron spicatum*) selected for greater food forb cover, total forb cover, and lower shrub heights; broods in altered big sagebrush/bunchgrass habitats selected greater tall grass cover and vertical cover height; broods in grassland showed no preference for any measured vegetation characteristics. During the early rearing period (post-hatching–6 wk) each year, broods selected sagebrush/bunchgrass. Broods in 1993 made greater use of grasslands than in 1992 and selected grassland during the late brood-rearing period (7–12 wk). Broods selected for sagebrush/bunchgrass during midday, but 52% of brood locations in the afternoon were in grassland. Tall grass cover was greater at morning (0500–1000 h) and afternoon (1501–2000 h) brood locations than at midday (1001–1500 h) and random locations. Midday brood locations had greater shrub cover and height than morning and afternoon locations. Selection of habitat components was similar to the results of other studies, but habitat conditions coupled with a possible lack of alternate brood-rearing cover types resulted in low survival of chicks.

Key words: broods, Centrocercus urophasianus, *habitat, Sage Grouse, Washington.*

Habitat use by Sage Grouse (*Centrocercus urophasianus*) for brood rearing was related to forb availability in previous studies (Peterson 1970, Oakleaf 1971, Autenrieth 1981, Drut, Crawford, and Gregg 1994, Drut, Pyle, and Crawford 1994). Sage Grouse chicks require protein-rich foods, including insects and forbs, for growth and development from hatching through approximately 3 mon (Savage 1969, Dunn and Braun 1986, Bergerud 1988, Drut, Pyle, and Crawford 1994). Changes in availability of these critical foods may affect Sage Grouse distribution and habitat selection (Wallestad 1971, Pyle 1993). Furthermore, in an Oregon study (Drut, Pyle, and Crawford 1994), Sage Grouse productivity was higher on an area where chicks fed on a diet of 80% forbs and insects than where chicks ate primarily (65%) sagebrush (*Artemisia* spp.).

Sage Grouse broods reportedly move from nesting habitats to sites where succulent and abundant forbs persist (i.e., meadows or upland sagebrush habitats) as summer temperatures increase and moisture decreases (Nelson 1955, Gill 1965, Savage 1969, Oakleaf 1971, Autenrieth 1981). Brood movements to these habitats are immediate or transitional depending on annual precipitation, temperature, and proximity from nesting habitat. Meadows and upland sagebrush habitats, however, often have been grazed excessively, causing reduced food and water availability (Savage 1969, Oakleaf 1971). Disturbance in these mesic habitats has increased soil erosion, facilitated invasion by exotic plants, affected vegetative composition, and lowered water table levels (Oakleaf 1971, Hofmann 1991). Oakleaf (1971) found fewer Sage Grouse foraging in Nevada meadows as food supplies diminished because of improper grazing practices and soil erosion. In Oregon, Drut, Crawford, and Gregg (1994) noted that broods used larger home ranges where forb availability is low than where forbs are relatively abundant. This may have resulted in reduced survival. These studies reveal the importance of forbs and insects in relation to abundance, distribution, habitat selection, and productivity. Nevertheless, the effect of massive landscape changes on habitat use by broods has rarely been documented. A full understanding of factors affecting habitat use by broods, especially where populations are severely depleted in areas of massive habitat changes, remains incomplete.

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We studied Sage Grouse in Washington where extensive habitat loss (approximately 70%) and alteration have reduced Sage Grouse to 2 separate populations totaling an estimated 630 birds by 1994 (Tirhi 1994). Our objectives were to examine selection of cover types by Sage Grouse broods and describe structure and composition of habitat components within cover types (3rd- and 4th-order selection, respectively; see Johnson 1980) used by broods.

STUDY AREA

The study was conducted on the Yakima Training Center (YTC), a 1058-km^2 area in Yakima and Kittitas counties, Washington, which supported approximately 330 Sage Grouse during this study (Tirhi 1994). Elevations on the YTC range from 183 to 1249 m. Hot, dry summers and cool, dry winters typify the study area. Growing season (September–August) precipitation for 1962–1993, obtained from the U.S. Department of Commerce Climatological Database, averaged 20.4 cm; growing season precipitation in 1991–92 and 1992–93 was 16.7 and 22.5 cm, respectively. Above normal precipitation accompanied by cooler than average temperatures began during winter 1992–93 and continued through summer 1993. These weather differences likely accounted for greater shrub cover and height and more tall grass and forb cover in certain cover types in 1993 (Sveum 1996).

Because the YTC serves as a military training ground, frequent off-road-vehicle use has resulted in approximately 5% of the area being covered by roads and trails (J.G. Stephan, Pacific Northwest Laboratory, personal communication). This disturbance has increased erosion and facilitated establishment of knapweed (*Centaurea* spp.) and cheatgrass brome (*Bromus tectorum*). Cattle and sheep grazing was initiated on the YTC in 1961; livestock stocking rates during 1992 and 1993 were 0.13 and 0.15 animal unit months/ha. Fires on the YTC, common during summer, burned 5.3 and 8.0 km^2 in 1992 and 1993, respectively (L.L. Cadwell, Pacific Northwest Laboratory, personal communication).

We identified 5 cover types available for brooding Sage Grouse on the YTC: (1) big sagebrush (*A. tridentata*)/bunchgrass, which is dominated by Wyoming big sagebrush (*A. t. wyomingensis*), rabbitbrush (*Chrysothamnus* spp.), bluebunch wheatgrass (*Agropyron spicatum*), and Sandberg's bluegrass (*Poa sandbergii*); (2) stiff sagebrush (*A. rigida*)/Sandberg's bluegrass; (3) altered big sagebrush/bunchgrass, which contains substantially more bare ground and lesser amounts of shrub and herbaceous cover because of repeated disturbance; (4) grassland, predominantly bunchgrasses with some rabbitbrush but virtually devoid of sagebrush because of frequent fires; and (5) riparian, with willow (*Salix* spp.), currant (*Ribes* spp.), grasses, sedges (*Carex* spp.), and Baltic rush (*Juncus balticus*).

METHODS

We captured Sage Grouse hens using spotlights and walk-in traps (Giesen et al. 1982, Schroeder and Braun 1991) and fitted the birds with numbered aluminum leg bands and necklace-attached radio transmitters during March 1992 and 1993. Each year, when radiotelemetry monitoring confirmed nesting completion, fate was determined by inspection of eggshell membranes or, in 3 instances (2 in 1992, 1 in 1993), observations of hens with young. Initial brood sizes were estimated from shells from successful nests, which were considered initial brood locations. We relocated radio-marked hens with broods ≥1 time/wk and attempted to obtain visual observations without flushing either hens or broods. If visual observations were not possible, we used recent sign (i.e., droppings, feathers) as an indication of habitat use. Each brood location was determined with a global positioning system in Universal Transverse Mercator (UTM) coordinates and marked with a flag to facilitate relocation for measuring vegetation. A brood was considered successful if ≥1 chicks were observed with a radio-marked hen after 1 August, the approximate date when brood integrity dissolves (Dalke et al. 1960, Oakleaf 1971). We used a *t* test to examine the null hypothesis that mean brood sizes were the same between years. Z tests with a continuity correction (Zar 1984:395–397) were used to test the null hypotheses that brood success rates and cover type use were the same between years.

We examined 3rd-order (selection of cover types) and 4th-order (selection of particular habitat components within cover types) habitat selection by hens with broods (Johnson 1980). Availability of cover types (3rd order) was determined within a composite minimum convex polygon home range (Odum and Kuenzler 1955) from pre-nesting movements of radio-marked hens with a geographic information system. Availability for 4th-order selection was identified by measuring randomly generated UTM coordinates within each cover type from the composite home range during the 1992–93 brood-rearing seasons.

We measured 4th-order characteristics of hens with broods at brood locations and random sites with 2 perpendicular 10-m transects at each location; the direction of the first transect was determined randomly. Canopy cover of all shrubs along each transect was estimated following Canfield (1941). Cover of grasses, forbs, and litter; residual cover; and bare ground were estimated along transects with ten 0.1-m^2 frames (Daubenmire 1959). Residual cover was defined as any dead upright plant material and consisted primarily of Russian thistle (*Salsola kali*), sagebrush, knapweed, and tumble mustard (*Sisymbrium altissimum*). Maximum height (cm) for shrubs and standing dead vegetation and droop height (excluding flowering parts) for grasses were measured. Grass height was classified as short (<18 cm) or tall (≥ 18 cm) following Wakkinen (1990) and Gregg et al. (1994). Vertical vegetation cover was measured at plot centers with a modified Robel pole (Robel et al. 1970). Four readings (2 each along the 2 perpendicular 10-m transects) were taken 4 m from the pole and 1 m in height.

Separate analyses were used according to brood age class: early (post-hatching–6 wk) and late (7–12 wk). Previous research revealed changes in habitat use and diets of chicks at approximately 6 wk of age (Martin 1970, Peterson 1970, Drut, Crawford, and Gregg 1994). Both 3rd- and 4th-order data in 1993 were apportioned into 3 diurnal periods: morning (0500–1000 h), midday (1001–1500 h), and evening (1501–2000 h). Too few broods were monitored in 1992 to analyze diurnal habitat selection. Primary forbs in the diets of Sage Grouse chicks in Oregon (Drut, Pyle, and Crawford 1994) and Idaho (Autenrieth 1981) were combined and called food forbs for 4th-order analysis. These forbs included milkvetch (*Astragalus* spp.), clover (*Trifolium* spp.), hawksbeard (*Crepis* spp.), microsteris (*Microsteris gracilis*), and species in the Cichorieae (milky-juiced composites). Riparian and stiff sagebrush/bluegrass cover types were combined for 3rd-order analysis because of infrequent brood use each year and were collectively called "other."

We compared cover types used by radio-marked hens with broods (observed) to the availability of each cover type (expected) with chi-square analysis for 3rd-order analysis. If a significant difference between use and availability was detected, Bonferroni simultaneous confidence intervals were calculated to identify which cover types were used disproportionately (Neu et al. 1974, Byers et al. 1984). The null hypotheses for 3rd-order selection were (1) broods used cover types during both early and late brood-rearing periods in proportion to their availability and (2) brood locations by diurnal period were in cover types in proportion to their availability.

Null hypotheses for 4th-order analyses were that (1) brood and random measurements within cover types did not differ, (2) there were no differences between early and late brood-rearing periods, and (3) there were no differences among times of day and random locations. Fourth-order data were treated with analysis of variance (ANOVA) for unbalanced data and protected least significant difference mean separation tests (Proc GLM, SAS Institute, Inc. 1989). Vegetation variables with nonnormal distributions were transformed (logit transformation for proportional data and log transformation for height data); however, nontransformed means and standard errors are reported herein. All statistical tests are 2-tailed and considered significant at $\alpha = 0.10$.

RESULTS

We captured and fitted 85 Sage Grouse hens with radio transmitters during March of both years (45 in 1992, 40 in 1993); 11 clutches were hatched in 1992 and 27 in 1993. Eggs hatched from 22 April to 28 May in 1992 and between 2 May and 19 June in 1993. More than 80% of clutches hatched in the big sagebrush/bunchgrass type. Initial brood size

TABLE 1. Availability and use (%) of cover types by Sage Grouse hens with broods during early and late brood-rearing periods on the Yakima Training Center, Yakima and Kittitas counties, Washington 1992–93.

		Brood-rearing locations (%)			
		1992		1993	
Cover type	Availability (%)	Early ($n^a = 22/5$)	Late ($n = 7/4$)	Early ($n = 68/17$)	Late ($n = 24/10$)
Big sagebrush/bunchgrass	46	77+[b]	71	68+	38
Grassland	34	9–	29	24	58+
Altered big sagebrush/bunchgrass	8	5	0	9	4
Other[c]	12	9–	0	0–	0–

[a] n = number of locations/broods.

[b] + = use greater than expected, no symbol = use in proportion to availability, – = use less than expected ($P < 0.10$) by Bonferroni confidence intervals.

[c] Includes riparian and stiff sagebrush/bluegrass.

TABLE 2. Availability and use (%) of cover types by Sage Grouse broods during 3 diurnal periods, Yakima Training Center, Yakima and Kittitas counties, Washington, 1993.

Cover type	Availability (%)	Morning[a] ($n = 18/12$)[b]	Midday ($n = 49/15$)	Afternoon ($n = 25/14$)
Big sagebrush/bunchgrass	46	67	65+[c]	44
Grassland	34	28	25	52
Altered big sagebrush/bunchgrass	8	5	10	4
Other[d]	12	0	0–	0

[a] Morning (0500–1000 h), midday (1001–1500 h), afternoon (1501–2000 h).

[b] n = number of locations/broods.

[c] + = use greater than expected, no symbol = use in proportion to availability; – = use less than expected ($P < 0.10$) by Bonferroni confidence intervals.

[d] Includes riparian and stiff sagebrush/bluegrass.

was greater in 1993 ($\bar{x} = 7.1$, $s_{\bar{x}} = 0.42$) than in 1992 ($\bar{x} = 5.7$, $s_{\bar{x}} = 0.50$, $t = -1.86$, $P = 0.07$). In 1992 only a single hen was known to recruit young (3 chicks) into the August population, but at least 11 broods ($\bar{x} = 1.5$ chicks) survived to 1 August in 1993. Several radio-marked hens entered a restricted area during each summer and the fate of broods that stayed in the restricted area (1 in 1992 and 4 in 1993) is unknown; consequently, they are not included in success estimates. An additional brood was removed in 1993 after contact was lost with the radio-marked hen. Brood success in 1993 was greater than in 1992 (10% in 1992 and 50% in 1993, $Z = -2.56$, $P = 0.01$).

We described 3rd-order selection by broods at 29 locations from 5 broods in 1992 and 92 locations from 19 broods in 1993. No 4th-order data were collected in 1992 because most broods perished shortly after hatching. Fourth-order data were collected from 72 locations from 17 broods and 30 random locations in 1993. Brood locations in 1992 were not analyzed by diurnal periods for 3rd-order selection because too few locations were obtained. The mean time between location of a brood and measurements for 4th-order characteristics was 4.6 d.

Sage Grouse selected big sagebrush/bunchgrass during early brood rearing of each year (Table 1) and used grasslands less than expected during the early rearing period of 1992. No cover-type selection was detected during the late rearing period in 1992, although 71% of locations were in big sagebrush/bunchgrass. During the late rearing period of 1993, broods selected grassland and used big sagebrush/bunchgrass in proportion to availability.

During the morning period in 1993, broods used all cover types in proportion to their availability (Table 2), but at midday they selected big sagebrush/bunchgrass. We found no selection during the afternoon period; however, 52% of locations were in grassland.

In 1993 brood locations in big sagebrush/bunchgrass had greater total forb and food forb cover and lower shrub heights than did random big sagebrush/bunchgrass locations (Table 3). Brood locations in altered big sagebrush/bunchgrass had greater tall grass cover

TABLE 3. Habitat characteristics of Sage Grouse brood and random locations by cover type on the Yakima Training Center, Yakima and Kittitas counties, Washington, 1993

	Big sagebrush/bunchgrass			Altered big sagebrush/bunchgrass			Grassland		
	Brood $(n = 43)$	Random $(n = 10)$		Brood $(n = 5)$	Random $(n = 10)$		Brood $(n = 24)$	Random $(n = 10)$	
Variable	$\bar{x}(s_{\bar{x}})$	$\bar{x}(s_{\bar{x}})$	P	$\bar{x}(s_{\bar{x}})$	$\bar{x}(s_{\bar{x}})$	P	$\bar{x}(s_{\bar{x}})$	$\bar{x}(s_{\bar{x}})$	P
Shrub cover (%)	14(2)	20(2)	0.12	7(4)	12(3)	0.39	4(2)	3(2)	0.88
Shrub height (cm)	18(2)	25(2)	0.10	11(7)	14(3)	0.70	5(2)	4(2)	0.75
Grass cover (%)									
Short, <18 cm	20(1)	20(2)	0.78	20(2)	19(2)	0.73	21(2)	23(3)	0.59
Tall, >18 cm	17(1)	19(4)	0.76	21(6)	8(3)	0.04	21(3)	15(2)	0.24
Forb cover (%)	25(2)	8(1)	<0.01	15(4)	21(6)	0.51	19(3)	14(4)	0.44
Food forb cover (%)	8(1)	2(1)	0.01	4(2)	3(1)	0.45	4(1)	3(1)	0.32
Residual cover (%)	1(0.2)	3(1)	<0.01	1(0.4)	1(1)	0.41	1(0.4)	1(0.5)	0.31
Residual cover height (cm)	1(0.3)	3(0.5)	0.03	2(1)	1(1)	0.77	2(0.5)	1(1)	0.24
Vertical cover height (cm)	15(2)	17(2)	0.26	17(4)	6(1)	0.01	9(1)	9(1)	0.94
Bare ground (%)	32(2)	35(4)	0.54	40(6)	49(4)	0.22	43(3)	47(5)	0.43
Litter (%)	57(3)	60(5)	0.67	46(4)	40(4)	0.43	44(3)	37(5)	0.19

and taller vertical cover height than random altered big sagebrush/bunchgrass locations. No differences were detected between brood and random locations in grassland. Food forb cover was greater at early and late brood locations than at random locations (Table 4).

Midday brood locations had greater shrub cover and shrub height than morning and afternoon brood locations (Table 5). Afternoon brood locations had less shrub cover and height than random locations. Morning and afternoon brood locations had greater tall grass cover than midday brood and random locations. During each diurnal period food forb cover was greater at brood locations than at random locations. Vertical cover was greater at midday brood locations than afternoon brood and random locations.

DISCUSSION

Broods exhibited similar patterns of cover-type use during the early rearing period each year by selecting big sagebrush/bunchgrass, which also was the primary nesting habitat. After hatching, before chicks can fly and when mortality is highest (Patterson 1952, Autenrieth 1981), broods need food in close proximity to escape cover. Random big sagebrush/bunchgrass locations had greater shrub cover and height than grassland and altered big sagebrush/bunchgrass. Short and tall grass cover also was abundant in big sagebrush/bunchgrass. The combination of shrub and grass cover in big sagebrush/bunchgrass apparently provided the best cover for nest success and early brood survival on the YTC.

Most late brood-rearing locations in 1992 were in big sagebrush/bunchgrass, but in 1993 late brood cover-type selection switched to grassland. Hens with chicks made greatest use of grasslands during the afternoon period. In Montana most early summer brood locations were in sagebrush-grassland types, but as forbs desiccated, grouse shifted to black greasewood (*Sarcobatus vermiculatus*) and grassland cover types in more mesic sites (Peterson 1970, Wallestad 1971). Savage (1969) found that broods left sagebrush uplands in Nevada during rapid temperature increases, which accelerated forb desiccation in sagebrush habitats. Broods may remain in sagebrush uplands when free water is available or during years when abundant precipitation increases forb availability (Oakleaf 1971, Dunn and Braun 1986).

Fourth-order analysis of 1993 data suggests that hens with broods in big sagebrush/bunchgrass (60% of all locations) selectively used sites with more total forbs (25% cover) and more food forbs (8% cover) than available randomly (8% and 2%, respectively). During early and late rearing periods, sites with greater amounts of key forbs were selected. Shrub height and residual cover were slightly less at brood locations than at random sites in big sagebrush/bunchgrass. In Oregon, Drut, Pyle, and Crawford (1994) found that total forb cover at brood sites, which ranged from 11% to

TABLE 4. Habitat characteristics of Sage Grouse brood locations during early and late brood-rearing periods and random locations on the Yakima Training Center, Yakima and Kittitas counties, Washington, 1993.

Variable	Early ($n = 53$) $\bar{x}(s_{\bar{x}})$	Late ($n = 19$) $\bar{x}(s_{\bar{x}})$	Random ($n = 30$) $\bar{x}(s_{\bar{x}})$
Shrub cover (%)	11(1)[a,b]	7(2)	12(2)
Shrub height (cm)	14(2)	9(3)	14(2)
Grass cover (%)			
Short, <18 cm	20(1)	20(3)	21(1)
Tall, >18 cm	19(2)	18(3)	14(2)
Forb cover (%)	22(2)	23(3)	15(3)
Key forb cover (%)	6(1)A	6(2)A	2(1)B
Residual cover (%)	1(0.3)A	0.6(0.2)A	2(0.4)B
Residual cover height (cm)	1(0.3)	1(0.3)	2(0.4)
Vertical cover height (cm)	14(2)	12(3)	11(1)
Bare ground (%)	35(2)A	39(3)A,B	44(3)B
Litter (%)	52(2)	50(4)	46(3)

[a] Means within row without letters or with the same letter are not significantly different ($P > 0.10$).
[b] Means within row with different letters are significantly different ($P \leq 0.10$).

14% during early brood rearing and from 19% to 27% during late brood rearing, influenced cover-type use. Likewise, Klebenow (1969), Schoenburg (1982), and Dunn and Braun (1986) found more forb cover at Sage Grouse brood locations than at random locations. Relatively low availability of forbs in big sagebrush/bunchgrass apparently resulted in strong selection by broods for forb-rich areas within this important brood-rearing cover type. Brood locations in altered big sagebrush/bunchgrass had greater tall (≥18 cm) grass cover and vertical cover than random locations within this cover type, suggesting that broods seek protective cover when using this less preferred cover type. No 4th-order vegetation selection was observed for grassland brood locations compared with random locations probably because forb cover was sufficiently abundant throughout and the abundant tall and short grass cover likely provided adequate concealment for escape.

Broods during midday selected big sagebrush/bunchgrass and were observed loafing and dust-bathing under large sagebrush. Midday brood locations had greater shrub cover, shrub height, and vertical cover than morning and afternoon locations. Midday brood locations also had greater vertical cover height than random locations. Several studies described grouse loafing during the midday after morning feeding (Nelson 1955, Gill 1965, Savage 1969, Oakleaf 1971, Autenrieth 1981). Broods used cover types in proportion to their availability during morning or afternoon periods, but 52% of afternoon locations were in grassland, which coincided with evening foraging. Morning and afternoon locations differed from midday and random locations by having greater tall (≥18 cm) grass and less shrub cover and height. Total forb cover and food forb cover at brood locations were not significantly different among diurnal periods. Daytime brood locations had greater forb and food forb cover than random locations. Dunn and Braun (1986) found that during the morning broods fed in open homogeneous areas and during the rest of the day used areas with more horizontal cover and greater variation in sagebrush canopy cover to roost and rest. Savage (1969) found that broods fed shortly after sunrise, loafed in sagebrush during midday, and moved to feeding areas in the evening. Fourth-order location measurements during the morning and afternoon suggested that broods left dense cover to feed, but total and food forbs were abundant at midday locations as well.

Late summer mean brood sizes from studies elsewhere ranged from 2.3 to 3.9 chicks/hen (Keller et al. 1941, Patterson 1952, Nelson 1955, Savage 1969, Wallestad and Watts 1973). Although brood success increased significantly on the study area in 1993, the number of chicks recruited/hen was lower than in other studies and may be insufficient to maintain population stability. Brood success was greater in 1993 than in 1992, which probably resulted from weather conditions during the 2 yr. More precipitation occurred in 1993, accompanied by cooler temperatures that lasted into the

TABLE 5. Habitat characteristics of Sage Grouse brood locations by diurnal period and random locations on the Yakima Training Center, Yakima and Kittitas counties, Washington, 1993.

	Diurnal period[a]			
Variable	Morning ($n = 13$) $\bar{x}(s_{\bar{x}})$	Midday ($n = 39$) $\bar{x}(s_{\bar{x}})$	Afternoon ($n = 20$) $\bar{x}(s_{\bar{x}})$	Random ($n = 30$) $\bar{x}(s_{\bar{x}})$
Shrub cover (%)	7(2)A,B[b,c]	15(2)C	4(1)B	12(2)A,C
Shrub height (cm)	9(2)A,B	18(2)C	6(2)B	14(2)A,C
Grass cover (%)				
Short, <18 cm	20(3)	19(1)	22(2)	21(1)
Tall, >18 cm	22(2)A	16(2)B	22(3)A	14(2)B
Forb cover (%)	21(3)	22(2)	22(4)	15(3)
Key forb cover (%)	6(1)A	7(1)A	6(1)A	2(1)B
Residual cover (%)	1(0.4)	1(0.3)	1(0.4)	2(0.4)
Residual cover height (cm)	1(0.4)	1(0.4)	2(0.5)	2(0.4)
Vertical cover height (cm)	11(1)A,B	16(2)B	9(2)A	11(1)A
Bare ground (%)	36(5)	36(2)	36(3)	44(3)
Litter (%)	51(4)	52(3)	52(4)	46(3)

[a] Morning (0500–1000 h), midday (1001–1500 h), afternoon (1501–2000 h).

[b] Means within row with different letters are significantly different ($P \leq 0.10$).

[c] Means within row without letters or with the same letter are not significantly different ($P > 0.10$).

summer. Increased precipitation in Nevada resulted in greater forb production, delayed plant desiccation, and possibly enhanced juvenile survival (Oakleaf 1971). Peterson (1970) found greater brood success during wet years in Montana when forb production was 2–3 times that of dry years. Autenrieth (1981) noted that migratory populations of Sage Grouse had high brood success because they were able to find forbs, whereas sedentary populations (like those at the YTC) had good reproductive success during moist years when forbs were abundant but did poorly during dry years. An increase in food and cover on the YTC in 1993 may have reduced brood movements, resulting in lower predator exposure and energetic costs of foraging. Nevertheless, by 1 August one-half of the broods were lost and the remainder declined from a mean of 7.1 to 1.5 chicks, approximately an 80% loss.

We concluded that nesting success (45%) was rather typical for Sage Grouse, but brood recruitment to 1 August (14%) and, especially, the number of chicks recruited (24 from 45 successful hens during the 2 yr) were far below average. We suggest that brood-rearing habitat was a strong limiting factor for this small population. Our results indicated that big sagebrush/bunchgrass and grasslands are important cover types throughout brood rearing. Within brood-rearing habitat, there was selection for sites with greater forb cover, especially forbs used as food, and shrub or grass cover (for concealment). Unlike many other Sage Grouse populations in western states, hens did not have the choice of alternative high-quality brood-rearing habitats, such as low sagebrush (*A. arbusula*), meadows, lakebeds, or broad, forb-rich drainages. Lack of these critical cover types at the YTC coupled with existing habitat conditions likely had an adverse effect on recruitment, which may limit populations on the YTC.

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SOIL-VEGETATION RELATIONS OF RECOVERING SUBALPINE RANGE OF THE WASATCH PLATEAU

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ABSTRACT.—On degraded subalpine range of the Wasatch Plateau, we examined the hypothesis that recovery of vegetation, as manifested by its composition and biomass yield, was related to soil phosphorus (P) and sulfur (S) status. We sampled 6 topographic locations to determine the relationship among composition and yield of grasses and forbs, litter cover, and soil characteristics including rock cover, organic carbon (C_o), total N (N_t), available nitrogen (N_{av}), total phosphorus (P_t), organic P (P_o), inorganic P (P_i), total potassium (K), total S (S_t), and element ratios. We also evaluated aspect effects. An alternative hypothesis was that productive potential was a function of depth of soil remaining after the period of destructive grazing. Differences among locations were significant for all vegetal attributes and for all soil characteristics except total K and C_o. Aspect was significant only for forb yield and P_t. Regression coefficients for yield and percentage composition of grasses were always opposite in sign to those for forbs. Yield and composition of grasses and forbs as groups were oppositely and strongly related to soil element ratios of C_o/P_t, N_t/P_o, C_o/P_t, and C_o/S_t but were not related to soil P_t or S_t. There was no clear support for acceptance of the hypothesis that soil P and/or S were major factors in recovery of this subalpine range after destructive grazing. Differences in regression coefficients and lower *r*-values among species within grass and forb groups, than for the groups themselves, to soil variables is a reflection of species individuality. This indicated a need to examine soil/vegetation relationships at the species level. Percentage compositions of grasses and forbs were oppositely related to the depth of A + B horizon, lending support to acceptance of the alternative hypothesis.

Key words: summer range, plant composition and cover, herbage yield, litter, soil C, N, P, S, and K.

After 35 years of destructive grazing by cattle and sheep in the late 1800s, the subalpine range of the Wasatch Plateau east of Ephraim, Utah, was in poor condition (Reynolds 1911, Sampson and Weyl 1918, Sampson 1919). Depletion of vegetation reached such severe proportions that most of the soil A horizon was lost by erosion and mud-rock floods were a common occurrence in the canyons and valleys below (Reynolds 1911, Croft 1967). In many places only subsoils remained when grazing regulation was begun with the 1903 establishment of the Manti National Forest (Reynolds 1911, Sampson and Weyl 1918, Ellison 1949). Transient livestock herds were abolished and livestock numbers greatly reduced, but most of the summer range was so badly deteriorated that these management changes were insufficient to halt continuing soil loss (Ellison 1954). Although condition of the range improved over the next 4 decades, most of the summer range was still unstable in 1950 and accelerated erosion was continuing, but at much reduced rates (Ellison 1954, Meeuwig 1960).

Our observations suggest that improvement in soil and vegetal conditions reached a plateau about 1930–1940, based on Ellison's (1954) records, and has remained essentially the same from the time of Ellison's studies (Intermountain Research Station, Provo, Utah, unpublished data; Johnson 1964). These observations led us to ask why, after 30–40 yr of rapid improvement under reduced grazing pressure, should secondary succession apparently stabilize at a midseral stage and remain so until the present?

There are perhaps several possible explanations for the apparent stable state (Lewontin 1969, Laycock 1991) that exists on the Wasatch summer range. Two explanations derive chiefly from degradation of the ecosystem and massive erosion that occurred over the long period of livestock overgrazing: (1) loss of most of the soil A horizon and hence most of the soil organic matter and nutrient capital, and alteration of nutrient cycling processes (Nikiforoff 1959, Anderson 1988); (2) loss of extinction-prone perennial grasses (Mack and Thompson 1982, O'Connor 1991), which are the key climax dominants in similar subalpine landscapes throughout the West, and were thought by Sampson (1919) to have dominated the pristine vegetation here.

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Although both explanations for the apparent static condition of soil-plant systems on the Wasatch summer range have merit, we focus on the former in this paper. More specifically, we hypothesized that losses of soil phosphorus (P) and/or sulfur (S) following the period of destructive grazing and erosion have diminished levels of one or both nutrients to the extent that accumulation of organic C and N to pre-degradation levels has been impeded (Walker and Adams 1958, Cole and Heil 1981). This in turn has limited soil development during range recovery. An alternative hypothesis was that neither P nor S was limiting relative to other elements, but that soil loss was so extensive that productive potential is now largely governed by the amount of remaining soil (i.e., A and B horizon). Under either hypothesis, regaining climax conditions of the former ecosystem would seem to require soil formation over a very long time to reestablish the original steady-state soil profiles characteristic of the pre-1870 climax soil-plant-nutrient system (Olsen 1958, Jenny 1980).

STUDY AREA

The study area is centrally located on the Wasatch Plateau about 17 km east of Manti, Utah. The area extends south 7 km from near the Alpine Station along Skyline Drive (Road 139) to Snow Lake. The long, narrow plateau is oriented approximately north and south with riblike ridges extending east and west. The plateau top is gently rolling, but gradient steepens (up to 65%) on slopes of east–west drainages. Average annual precipitation is about 840 mm; 2/3 of this falls as snow between November and April. Precipitation averages 173 mm during summer months (June through September) but varies considerably. Mean annual temperature is about 0°C (Ellison 1954). During the growing season (May through October), average maximum temperature is 21°C; average minimum is –5°C (Ellison 1954).

Soil parent materials are of the Flagstaff formation (Stanley and Collinson 1979) that outcrop over about 7200 km^2 in central Utah (Schreiber 1988). The dominant lithology is freshwater lacustrine limestone and calcareous shales with minor interbeds of sandstone, oil shale, conglomerate, gypsum, and volcanic ash (Weber 1964, Schreiber 1988). Soils of the plateau are mostly fine, mixed argic Cryoborolls, but lithic, pachic, and vertic Cryoborolls also are present. They are shallow to moderately deep; subsoils are silty clays or clay loams. Thickness of the A horizon averages just 4 cm; that of the B horizon averages 52 cm (range 30–74 cm). Based on typical profile descriptions (H.K. Swenson, Natural Resources Conservation Service, Boise, ID, personal communication), these relative horizon thicknesses indicate that much of the original A horizon was lost by wind and water erosion following the period of unrestricted grazing prior to 1903.

Vegetation of the Wasatch Plateau is chiefly herbaceous, but patches of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) occupy steep northerly exposures of east–west ridges and dot the plateau landscape. Because remnants of pristine vegetation do not exist (Ellison 1949, 1954), opinions differ regarding its exact character. Ellison (1954) described the original herbaceous community as mixed-upland herb dominated by tall forbs, while Sampson (1919) considered wheatgrasses (*Agropyron* spp.) the primary climax dominants.

METHODS

The original strategy for testing the hypotheses was a comparative analysis of paired eroded and uneroded soil-plant systems at various locations. However, after an exhaustive search, it was apparent that grazing use of this summer range had been so complete during the period of devastation that uneroded sites were nonexistent, even on plateaus isolated by steep terrain that we believed would limit access to livestock.

Instead, we selected 6 topographically separated locations, mostly small knolls, and sampled soil and plant attributes on up to 4 aspects. All 6 locations had a similar grazing history until the 1930s. Since then Elk Knoll (EK) and Alpine Cattle Pasture (CP) have been protected from livestock. Ideally, this would give us an array of site conditions that would permit differentiation among locations and aspects based on soil, parent material, and vegetation properties, and permit determination of key variables influencing herbage composition and production on the summer range.

On each location we attempted to restrict aspect sampling points to a single parent material stratum; hence, elevation among aspects was near constant. However, this was probably futile. Because individual parent material strata were usually very thin (≤0.5 m; Klemmedson and Tiedemann 1994), there was little confidence in sampling the same parent material among all aspects of a location. All locations were within 7 km of each other. Northeast, SE, SW, and NW aspects were sampled on Elk Knoll (EK; elevation 3116 m) and a knoll adjacent to Snow Lake (SL; elevation 3133 m). Two aspects were sampled on Trail Ridge (TR; elevation 3216 m), Skyline Drive (SD; elevation 3200 m), and Alpine Cattle Pasture (CP; elevation 3066 m); a single aspect was sampled on South Knoll (SK; elevation 3109 m). Slope gradient was 10–30% among aspects on SL; gradients were <5% on other locations.

We sampled at selected aspects from randomly located soil pits and vegetal-litter-cover plots. Soil pits were dug and profiles described by standard terminology. Single samples of known volume were taken from each horizon (3–5 above the C or R horizon) for laboratory analysis. Herbage and litter were sampled in 6 randomly located 0.5-m^2 plots near each pit. Basal cover of litter, bare ground, and rock, and foliar cover by species were visually estimated; mass of grasses, forbs, and litter was determined by harvesting each component separately, followed by oven-drying (70°C) and weighing.

For chemical analyses we air-dried soils, sieved them to remove the >2-mm fraction, and then ground them to pass a 150-μm sieve. Samples were analyzed for total C by dry combustion (Nelson and Sommers 1982) in a LECO high-frequency induction furnace (LECO Corp., St. Joseph, MI). Organic C (C_o) of soils was determined by difference after determining carbonate by a gasometric method (Dreimanis 1962). Total N (N_t) was determined by semi-micro-Kjeldahl (Bremner and Mulvaney 1982) and total S (S_t) by dry combustion in the LECO high-frequency induction furnace (Tiedemann and Anderson 1971). Total soil P (P_t) was determined using ascorbic acid color development (Olsen and Sommers 1982) following hydrofluoric acid digestion (Bowman 1988). Inorganic P (P_i) was determined with the same color development on samples ignited at 550°C for 2 h (Olsen and Sommers 1982), while organic P (P_o) was determined by difference. Available nutrients (X_{av}) were determined as follows: P by ascorbic acid color development following 0.5 M sodium bicarbonate extraction (Olsen and Sommers 1982), N by steam distillation of 2 N KCl extracts (Keeney and Nelson 1982), and S with 1:1 water extracts, followed by ion chromatography (Dick and Tabatabai 1979).

To facilitate comparison among sites and aspects, we summarized soil horizon data and expressed the data for the 0- to 15-cm soil layer and for the entire solum. The data were analyzed by 2 ANOVAs: 1 for EK and SL knolls with data for all 4 aspects, the 2nd with data from all 6 locations, where the number of aspects sampled was unequal. In the latter ANOVA the interaction term was calculated using data only for EK and SL locations. Backward (stepwise) multiple regression analysis was used to relate herbage yield and composition to soil surface and 0- to 15-cm soil layer properties.

RESULTS AND DISCUSSION

Location and Aspect Differences

VEGETATION AND SOIL COVER.—Analysis of variance for all locations showed significant differences among locations for 6 attributes of vegetation and cover at the $P \leq 0.05$ level (Table 1). Of these, forb yield was the only attribute that also differed significantly among aspects (Table 1); it was highest on NW aspects and lowest on NE and SE aspects (Table 2). The significant location response of forb composition (by foliar cover) must be qualified because of the significant Location × Aspect interaction (Table 1). Forb composition responded differently to aspect at EK and SL locations, especially on SE and SW aspects (Table 2). This response may, at least in part, be influenced by parent material at the SL location. In a companion study (Klemmedson and Tiedemann 1998), parent material was highly associated with vegetal properties.

Based on values for the 6 vegetation and cover attributes discussed above, the locations appear to form 2 distinct groupings (Fig. 1). The EK, CP, and SK locations were similar for

TABLE 1. Probability values from analysis of variance for all locations, and for Elk Knoll (EK) and Snow Lake (SL) locations alone.

	Probability values				
	All locations			EK and SL	
Variables	Location	Aspect	L × A	Location	Aspect
VEGETATION AND SURFACE COVER					
Total yield (g/m^2)	0.033	NS	NS	NS	NS
Forb yield (g/m^2)	<0.001	0.038	NS	0.004	NS
Grass composition (%)	0.036	NS	NS	0.090	NS
Forb composition (%)	0.034	NS	0.050	0.090	NS
Bare ground (%)	0.006	NS	NS	NS	NS
Rock cover (%)	0.029	NS	NS	0.004	NS
SURFACE SOIL, 0–15 CM					
Organic C (kg/m^2)	0.071	NS	NS	0.053	NS
Available N (g/m^2)	<0.001	0.099	NS	NS	NS
Total P (g/m^2)	0.009	0.010	NS	0.002	0.049
Inorganic P (g/m^2)	0.010	0.069	NS	0.013	NS
Organic P (% of total)	0.013	NS	0.010	0.047	NS
Total K (kg/m^2)	NS	NS	NS	0.019	NS
C_o/P_t	0.004	NS	NS	0.005	NS
C_o/S_t	0.007	NS	NS	0.001	NS
N_t/P_t	<0.001	NS	NS	0.001	NS
N_t/P_o	0.002	NS	NS	0.138	NS

TABLE 2. Influence of aspect on forb yield, and interaction of location and aspect on forb composition by foliar cover.

	Aspect				
	NE	SE	SW	NW	LSD*
Forb yield (g/m^2)	75	76	98	128	24
Forb composition (%)					17
Elk Knoll	67	84	87	90	
Snow Lake	61	53	28	72	

*$P < 0.05$.

composition of grasses and forbs, less so for cover of bare ground and rocks, and differed in herbage yield (Fig. 1). Yield of forbs and total herbage for the EK and CP locations was similar, and much greater than that for the SK location. Herbage yield at all 3 locations was dominated by forbs (>80% of yield and composition). These locations had little exposed rock (<5%) and moderate amounts of bare ground (13–26%).

The SL, TR, and SD locations form the 2nd group. They were similar to each other for most attributes, especially yield of forbs and composition of grasses and forbs (Fig. 1). They had significantly lower total herbage yield than the EK and CP locations and vegetal composition was about equally divided between grasses and forbs. These locations (SL, TR, and SD) all had large amounts of bare ground and exposed rock (Fig. 1).

The 6 locations break out into the same groupings based on species composition. Of the 25 species comprising at least 3% of the composition (Table 3), only 2 grasses (*Agropyron trachycaulum* and *Stipa lettermani*) and 1 forb (*Achillea millefolium*) occurred on all 6 locations. Composition of these 3 species was similar among the SL, TR, and SD locations, and from 2.0- to 6.6-fold higher than that for the EK, CP, and SK locations. The 2 groups of

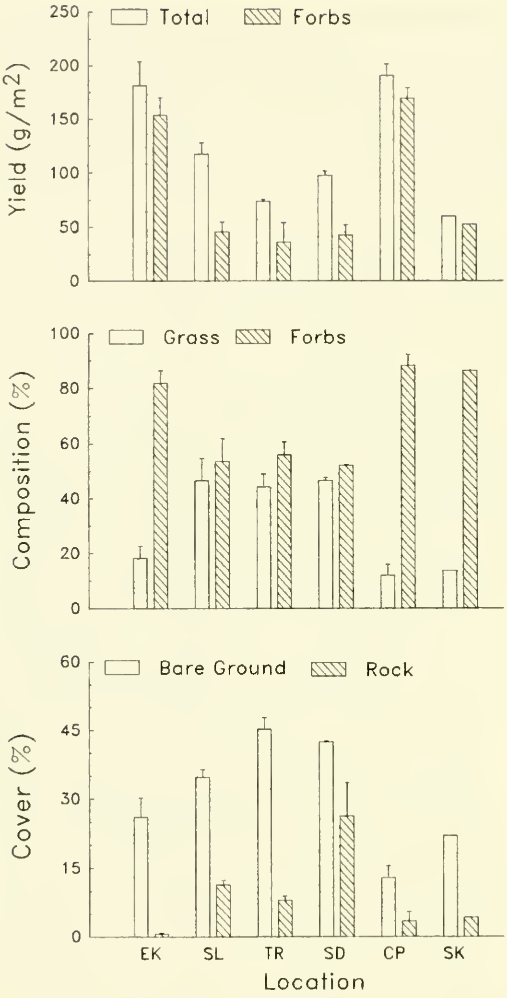

Fig. 1. Effect of location on yield of forbs and total vegetation, composition (by foliar cover) of grasses and forbs, and cover of bare ground and rocks.

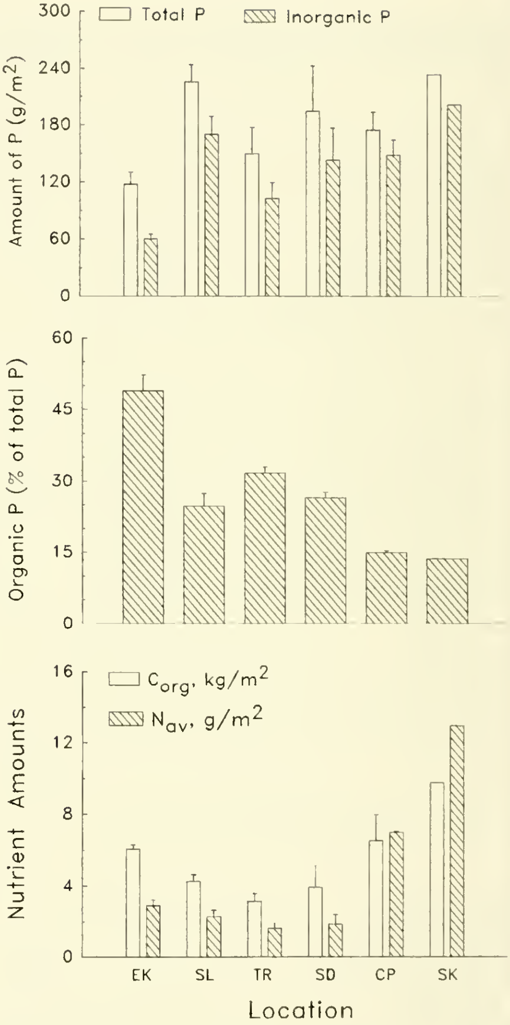

Fig. 2. Effect of location on amounts of total and inorganic P, percentage organic P, and amounts of organic C and available N in soils.

locations also differed in distribution of several forbs. Six species (*Aster foliaceus* v. *canbyi*, *Erigeron speciosus*, *Geranium fremontii*, *Ligusticum porteri*, *Penstemon rydbergii*, and *Potentilla gracilis*) were found only on the EK, CP, and SK locations (at least 2 of the 3 locations), while 2 species (*Artemisia ludoviciana* v. *incompta* and *Cymopterus lemmonii*) occurred only on the SL, TR, and SD sites (Table 3). In a companion study on the SL location (Klemmedson and Tiedemann 1998), *C. lemmonii* was highly associated with rocky sites with shallow soils of low nutrient content.

SOIL PROPERTIES.—Nine properties of the 0- to 15-cm soil layer differed significantly among the 6 locations (Table 1). Differences were significant at the $P \leq 0.01$ level for N_{av}, P_t, P_i, and the C_o/P_t, C_o/S_t, and N_t/P_t ratios, at the $P \leq 0.05$ level for percentage P_o, and at $P \leq 0.10$ for C_o. In the case of P_o content as a percentage of P_t, there was a significant L × A interaction (Table 1): P_o was markedly higher at the EK than the SL location for all aspects except SW.

Results of the analysis of variance for EK and SL locations alone (Table 1) were similar to that for all locations, with 2 exceptions. These 2 locations did not differ significantly in

TABLE 3. Species composition (%) at 6 knoll locations[a].

Vegetal component	Knoll location[b] EK	SL	TR	SD	CP	SK
GRASSES AND GRASSLIKE						
Agropyron trachycaulum	7.6	10.5	13.1	8.9	3.6	3.4
Alopecurus pratensis						3.4
Carex microptera	3.6					
Stipa columbiana		6.7				
Stipa lettermani	3.8	28.2	30.5	36.6	5.2	6.0
Others	3.2	1.0	0.6	2.7	3.0	0.8
Total	18.2	46.4	44.2	48.2	11.8	13.6
FORBS AND SHRUBS						
Achillea millefolium ssp. *lanulosa*	8.4	12.6	15.0	11.3	5.8	5.6
Artemisia ludoviciana v. *incompta*		18.8	4.7	19.7		
Aster foliaceus v. *canbyi*	13.6					
Astragalus miser v. *oblongifolius*			3.0			
Castilleja sulphurea					4.6	5.2
Cymopterus lemmonii		5.2	9.8	10.6		
Erigeron speciosus	5.3				4.9	3.4
Erigeron ursinus			8.2			
Geranium fremontii	13.5				22.4	
Lesquerella utahensis				3.3		
Ligusticum porteri	5.2				8.2	
Penstemon rydbergii	10.9				4.4	3.6
Potentilla glandulosa			3.4			
Potentilla gracilis	3.1				10.8	
Solidago parryi						55.2
Swertia perennis	3.0					
Taraxacum officinale		4.6	6.5			
Valeriana occidentalis					4.2	3.6
Vicia americana v. *americana*		6.4			4.6	
Vicia nuttallii v. *nuttallii*					5.8	
Others	18.8	6.0	5.2	6.9	12.6	9.8
Total	81.8	58.6	55.8	51.8	88.3	86.4

[a] Based on foliar cover, species with <3% composition not listed.

[b] See text for names and descriptions of locations.

N_{av}, but they did differ in total K. Moreover, there was a significant L × A interaction for P_t. Although P_t was higher at SL than at EK (Fig. 2), the absolute and proportional differences were a function of aspect.

For soil properties, the 6 locations did not break out into the 2 groups observed for vegetation and cover attributes. Those groupings were apparent only for 1 of the 9 soil properties (C_o/P_t ratio) found to differ among locations (Fig. 3). Analysis of data for variables of the entire solum added very little information to that shown for the 0- to 15-cm soil layer and hence are not shown here.

Vegetation-Soil Relations

The marked differences described above in vegetal attributes and soil properties among locations caused us to pursue further soil-vegetation relations that might explain vegetational differences among locations (Fig. 1, Table 3) and give clues to the seral plateau these systems have been in for the past 50 yr. Simple linear regression relating vegetal attributes with soil properties, especially those shown to be significant in Table 1, indicates that grasses and forbs, as groups, responded differently, but consistently, to these variables (Table 4). In fact, for each independent variable shown in this table for regressions with herbage yield and composition as dependent variables, the regression coefficients for grasses were always opposite in sign to that for forbs. Certainly, this was not the case for all independent variables we sampled, but for the large majority the trend was very noticeable.

In a companion study at the SL location (Klemmedson and Tiedemann 1998), the dominant grass (*Stipa lettermani*) and forb (*Cymopterus lemmonii*) were oppositely related for

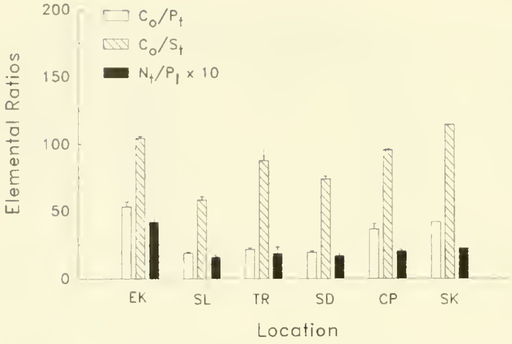

Fig. 3. Effect of location on elemental ratios of soil.

every variable sampled. But, for groups of grasses and forbs comprising many species (Table 3), it is remarkable that these groups would respond in an opposite manner so consistently to various growth (soil/site) parameters, although not always with high *r*-values (Table 4). That correlation coefficients associated with specific independent variables in Table 4 were not high, as a rule, is a reflection of the individuality of species within grass and forb groups in response to location and aspect. Figure 4 illustrates this individuality of 2 grasses and 2 forbs in their response to C_o/P_t and C_o/S_t, variables that were both highly correlated with grass and forb composition (Table 4). Contrasting responses of grass and forb groups also have been observed by Huenneke et al. (1990) in short-term fertilization experiments on serpentine soils. Within vegetal groups having common properties, species responded to experimental treatments in an individualistic manner. Also, Chapin and Shaver (1985) observed this kind of species-community behavior in response to manipulation of environment in tundra.

Of those variables one would ordinarily associate with soil fertility, only C_o and the 2 element ratio variables were correlated with yield and composition (Table 4). The high *r*-values for percentage litter cover and rock cover are at first puzzling. However, when one considers the extent of correlation usually observed among soil-plant-litter properties, both positively and negatively, high *r*-values for soil surface variables (Table 4) are not surprising. Moreover, these soil surface variables may be expressing the influence of soil physical properties that we did not sample, but which may have significantly influenced vegetal yield and composition.

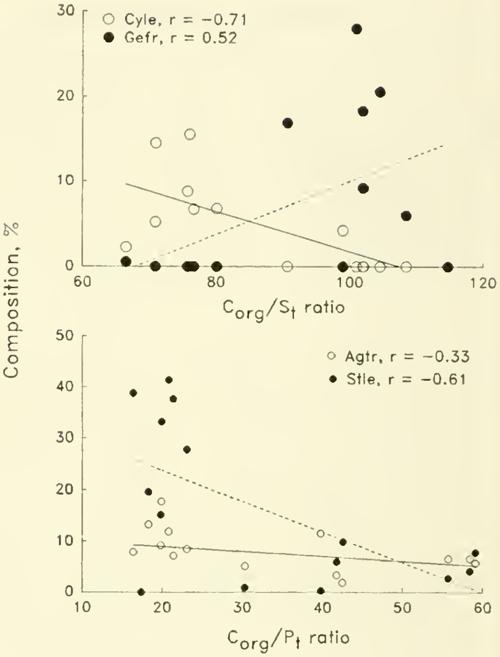

Fig. 4. Relationship of composition (by foliar cover) of *Cymopterus lemmonii* and *Geranium fremontii* to C_o/S_t ratio and composition of *Agropyron trachycaulum* and *Stipa lettermani* to C_o/P_t ratio.

Table 5 summarizes our attempt to predict herbage yield and composition with 2-variable equations using backward multiple regression. Overall, percentage rock cover was the most efficient predictor of yield and composition of both grass and forbs, based on standardized regression coefficients. Percentage litter cover and bare ground were about equal as predictors of total yield. P_o was as efficient as soil surface features only in the grass yield equation. When a 3rd variable was allowed in the equation (3-variable equations not shown), P_o filled that role in 4 of 5 cases, based on variation explained. In the 3-variable grass yield equation, C_o became the 3rd and most efficient variable. That variables portraying soil surface features would appear as the most efficient predictors of vegetal yield and composition in multiple regression is not surprising in view of results from simple regression (Table 4) and suggests a high degree of intercorrelation with soil properties more commonly associated with productivity.

TABLE 4. Contrasting regression relations between yield and composition of grasses and forbs and several independent variables.

Dependent variables	Independent variables	Regression coefficient		Correlation coefficient	
		Grass	Forbs	Grass	Forbs
Yield (g/m^2)	Organic C (g/m^2)	–7.176	25.158	–0.43	0.68**
	Total N (g/m^2)	–0.090	0.234	–0.30	0.40
	Total P (g/m^2)	0.146	–0.416	0.27	–0.40
	Total S (g/m^2)	–0.431	0.799	–0.25	0.24
	C_o/P_t	–1.273	2.895	–0.63*	0.73**
	N_t/P_o	–6.627	14.116	–0.64*	0.67**
	Rock cover (%)	3.356	–9.188	0.58*	–0.81**
	Litter cover (%)	–0.051	4.123	–0.13	0.76**
Composition[a]	Organic C (g/m^2)	–5.993	5.940	–0.54*	0.54*
	Total N (g/m^2)	–0.079	0.076	–0.49	0.49
	Total P (g/m^2)	0.087	–0.092	0.28	–0.29
	Organic P (g/m^2)	0.435	–0.449	0.42	–0.43
	C_o/P_t	–0.881	0.890	–0.74**	0.74**
	C_o/S_t	–0.820	0.830	–0.69**	0.70**
	Rock cover (%)	2.686	–2.754	0.79**	–0.80**

*Significant at $P < 0.05$.
**Significant at $P < 0.01$.
[a] Based on foliar cover.

TABLE 5. Statistics from backward multiple regression predicting herbage yield and composition (based on foliar cover) with 2-variable equations.

Herbage component	Variables	Standardized coefficient	Probability of significant *F*	*R*-square
YIELD				
Total	Regression		0.002	0.72
	Litter cover	0.238	0.001	
	Bare ground	–0.216	0.067	
Grass	Regression		0.026	0.52
	Rock cover	0.493	0.024	
	Organic P	0.454	0.085	
Forbs	Regression		0.001	0.76
	Litter cover	0.408	0.001	
	Rock cover	–0.553	0.021	
COMPOSITION				
Grass	Regression		0.007	0.63
	Litter cover	–0.094	0.016	
	Rock cover	0.730	0.015	
Forbs	Regression		0.005	0.64
	Litter cover	0.092	0.013	
	Rock cover	–0.744	0.012	

We demonstrated strong association between grass- versus forb-dominated vegetation and several soil nutrient and surface soil properties. On the whole it appears that forbs responded positively to variables generally associated with better growing conditions, and the opposite for grasses. Moreover, results demonstrate marked differences among the 6 study locations based on these soil-plant relations. Although vegetation was strongly associated with P, and to a lesser extent S, it seems premature to accept the primary hypothesis regarding the importance of P and S. The opposite relationship of grasses and forbs to depth of A

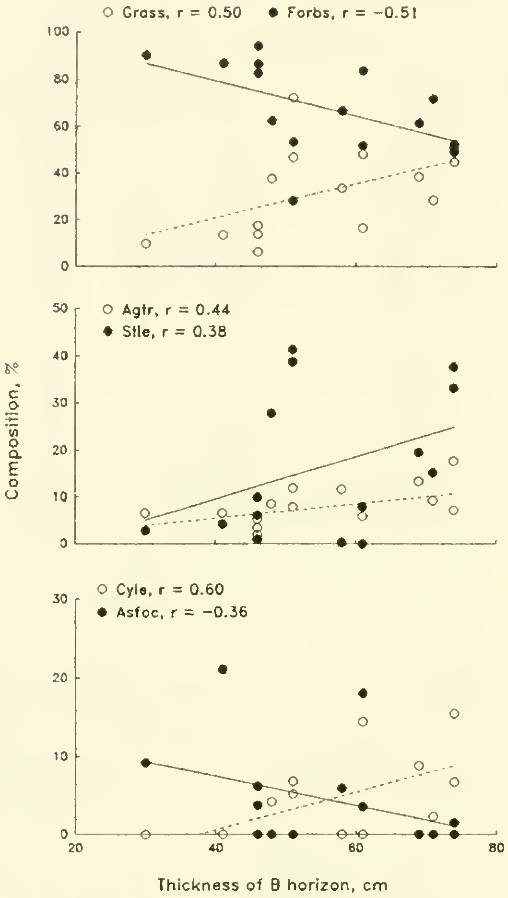

Fig. 5. Effect of thickness of A + B horizon on composition (by foliar cover) of grasses, forbs, *Agropyron trachycaulum, Stipa lettermani, Cymopterus lemmonii,* and *Aster foliaceus* v. *canbyi*.

and B horizon (Fig. 5) supported the alternate hypothesis that plant attributes are governed by depth of soil remaining after the period of destructive grazing. It is also apparent from the differential response of individual species within each group (Fig. 5) that these relationships are not straightforward.

We believe soil and plant attributes that distinguish the 6 locations were primarily a reflection of the parent materials and the soil that remained (mainly B horizon) after many years of destructive grazing and severe erosion. Differences among soils, which in this case were chiefly a function of differences in composition of parent material, were manifested in soil-vegetation relationships established here. All 6 sites were unprotected during the period prior to 1905, and they appear to have suffered more or less equally, losing 50–90% of the A horizon (Klemmedson and Tiedemann 1994). Grazing over the past 80 yr differed among the 6 locations; EK and CP have been reasonably well protected since the 1930s. But the impact of differential grazing since 1905, though marked in the case of EK and CP locations, appears to be small compared to the differences among sites coupled with the earlier loss of so much of their productive capacity through erosion.

CONCLUSIONS

Although we demonstrated strong relationships among several soil and vegetal properties, cause-and-effect relationships were not forthcoming from this information. Comparisons with undisturbed areas would perhaps have provided such linkages. Nonetheless, it is apparent that yield and composition of vegetation were closely tied to soil properties. Of the physical properties, rock cover was the best predictor of yield and composition of grasses and forbs. Litter cover was the best vegetal attribute for predicting forb yield and composition. Of the soil chemical characteristics, the C_o/P_t ratio was the best predictor of forb and grass yield and composition.

The opposite response of grasses and forbs as groups, as indicated by regression coefficients, to all measured attributes suggests that these 2 groups occupy different seral positions in successional development of this area. Their roles in successional dynamics are not clearly defined and will require more careful study of their responses to soil development. Contrasting responses of individual species within plant groups (Figs. 4, 5) suggest the need to focus on species-level responses. In a companion study we are attempting to do this by examining foliar cover response to fertilization with 5 combinations of N, P, K, and S for about 100 species over a 5-yr period.

Depth of remaining soil, over 90% B horizon, has not been emphasized in earlier studies of this area but may be an important determinant in the composition of grasses and forbs as plant groups. Depth of B horizon varied widely among sites and locations and may be a primary reason that location was such an important factor in the analysis.

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UNDERSTORY PATTERNS IN CUT WESTERN JUNIPER (*JUNIPERUS OCCIDENTALIS* SPP. *OCCIDENTALIS* HOOK.) WOODLANDS

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ABSTRACT.—Western juniper (*Juniperus occidentalis* spp. *occidentalis*) has rapidly expanded into shrub steppe communities in the Intermountain Northwest during the past 120 yr. Cutting juniper is a management tool used to restore shrub steppe communities. Response of the understory after cutting is strongly influenced by plant species composition existing prior to treatment. This study assessed distribution patterns of understory plants over 2 growing seasons after tree cutting in a western juniper woodland. Cover, density, and diversity of understory species were compared among 3 locations: interspaces, duff zones (previously under tree canopies), and debris zones (beneath cut trees). Plant cover and density increased in all zones following tree cutting. Understory vegetation in cut woodlands exhibited strong zonal distribution. Cover and density of *Poa sandbergii* and *Sitanion hystrix* and canopy cover of annual forbs were greatest in duff zones ($P < 0.05$). Density and cover of other perennial grasses and total densities of perennial forbs and annual forbs were greatest in interspaces ($P < 0.05$). Debris zones tended to have the lowest overall understory cover and plant density values. Under juniper debris many species common to interspaces were reduced in density, although plants that survived or established beneath debris grew larger than their counterparts in interspaces. Species that increased in density and cover under debris were plants characteristic of duff zones and whose seeds are typically wind dispersed.

Key words: western juniper, understory patterns, diversity, juniper debris, species composition, zonal succession.

Pinyon-juniper woodlands in the western United States have rapidly expanded into shrub-grasslands since the late 1800s (Tausch et al. 1981, West 1984, Miller and Wigand 1994). Western juniper (*Juniperus occidentalis* spp. *occidentalis* Hook.) has invaded extensive areas of sagebrush-grasslands and other plant communities in the Pacific Northwest (Burkhardt and Tisdale 1969, Miller and Rose 1995). The transition from shrub steppe communities to woodlands has resulted in reduced understory productivity and diversity (Johnson 1962, Jameson, 1967, Burkhardt and Tisdale 1976, Tausch et al. 1981, Tausch and Tueller 1990, Bates 1996). Understory distribution patterns in canopy and interspace zones become more distinctly developed during woodland development (Johnson 1962, Pieper 1990, Vaitkus and Eddleman 1991). Understory patterns probably reflect a mosaic of canopy and interspace microenvironments. Junipers influence the microenvironment under tree canopies by modifying temperatures and light levels (Pieper 1990), accumulating soil nutrients (Doescher et al. 1987, Bates 1996), intercepting precipitation (Larsen 1993), and causing physical or allelopathic interference by litter layers (Jameson 1966, Peterson and Buss 1974). Padien and Lajtha (1992) attributed understory spatial patterns in pinyon-juniper woodlands to differences in nutrient availability, shade protection, seed dispersal, and seed germination.

Management prescriptions employed to reduce western juniper dominance in rangelands have been successful in increasing understory productivity and cover (Evans and Young 1984, Vaitkus and Eddleman 1987, Rose and Eddleman 1994, Bates 1996). However, the influence of spatial distribution on plant succession following juniper elimination, particularly with removal methods that leave substantial amounts of juniper debris on site, are poorly documented.

Evaluating understory distribution patterns may prove useful in generating hypotheses on species-zonal interactions and in predicting successional responses and pathways following juniper control. This study was designed

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(1) to assess understory distribution patterns within an intact western juniper woodland prior to tree cutting and (2) to evaluate the effects of tree cutting on understory zonal patterns.

METHODS

Study Site

The study was conducted on Steens Mountain in southeastern Oregon, 9.5 km southeast of Diamond (118°36′W, 42°55′N). Elevation at the site is 1525 m and aspect is west-facing with a 22% slope. The site is dominated by an 80-yr-old western juniper woodland. Juniper canopy cover averaged 23%, and tree density averaged 228 trees ha^{-1}. The following indicated a fully developed juniper stand: limited terminal and lateral leader growth on juniper trees, lack of juniper seedling recruitment, and most *Artemisia tridentata* spp. *vaseyana* Nutt. (mountain big sagebrush) were dead. Understory perennial plant basal cover averaged 2.5% in interspaces and 2.9% under tree canopies. Based on existing shrub/understory vegetation, soils, and aspect, we judged the original community, prior to woodland dominance, to have been *Artemisia tridentata* spp. *vaseyana/Stipa thurberiana* type.

Prior to treatment the dominant understory plant was *Poa sandbergii* Vasey (Sandberg's bluegrass), comprising nearly 75% of the total understory perennial plant basal cover. Other species characteristic of the site included *Stipa thurberiana* (Thurber's needlegrass), *Sitanion hystrix* (bottlebrush squirreltail), *Agropyron spicatum* (bluebunch wheatgrass), *Astragalus filipes* (basalt milkvetch), *Microsteris gracilis* (microsteris), and *Alyssum alyssioides* (pale alyssum).

Soils were classified as clayey-skeletal, montmorillonite, frigid Lithic Agrixerolls. They are shallow (40–50 cm deep) and are underlain by a thick, welded ash layer of rhyolite and rhyodacite composition, which limits root penetration.

Domestic livestock grazing has occurred on this site since the late 1800s. The ridge on which the study site is located was used as a sheep wintering area through the 1930s. Since the 1940s the site has been grazed by cattle in the early spring (April). Livestock were excluded from the site during our study.

Climate in southeastern Oregon is semiarid and continental. Winter and spring are typically cool and wet; summers are warm and dry. The majority of annual precipitation falls between November and June. Mean water year (1 October–30 September) precipitation at weather stations located 27 km southwest (elevation 1300 m) and 30 km northwest (1250 m) of the site average 28.2 and 24.9 cm, respectively.

Experimental Design and Measurements

In June 1991 we established eight 0.8-ha replicated plots along the contour of the ridge slope. Plots were selected for similarities in overstory/understory cover and density, soil type, and aspect. After being measured for baseline vegetation characteristics (basal cover and density), juniper trees were felled with chainsaws in August 1991 on half of each plot (0.4 ha). Cut trees remained on the plots. We began subsequent measurements of understory characteristics and soil moisture content in April 1992 and concluded in September 1993. In this paper we report data from the cut plots only in order to highlight zonal differences.

Understory measurements were canopy and basal cover, density, and diversity. Sampling was spatially separated into 3 zones: duff, juniper debris, and interspace. Duff zones are defined as those areas formerly beneath tree canopies with a surface layer of old juniper needle litter. Debris zones are former interspace zones that are covered by felled juniper trees. Interspace zones are open areas that are not influenced by old or newly felled juniper tree litter.

We estimated understory plant density (1991–1993) and canopy cover (1993 only) for each zone in each replicate, in the 4 cardinal directions (for duff and interspace zones only), around 12 trees per replication, using a 30.5 × 61-cm frame (48 subsamples per zone per replication). Trees were randomly selected each year. For the debris zone we estimated density and cover by randomly subsampling 4 locations under each of the 12 cut trees in each replication. We subsampled along the outer 1/3 of the duff zone. Interspace zones were located approximately 3 m from the outer edge of the duff zone or at the midpoint between duff zones.

Using the cover class technique described by Daubenmire (1959), we estimated canopy cover.

In this study 7 cover classes were designated: trace (0–1%), I (1–5%), II (5–25%), III (25–50%), IV (50–75%), V (75–95%), and VI (95–100%). Midpoints of cover classes were used for statistical analysis.

Understory basal cover of perennial grasses and forbs was measured along five 30.5-m line intercepts positioned parallel to the slope in all 8 cut plots in 1991 (baseline year, prior to cutting), 1992, and 1993. Transects were permanently marked in 1991 using rebar stakes. Groundcover provided by juniper debris and old juniper litter in duff locations was also estimated along the transects.

Gravimetric soil water content was sampled in interspace and debris zones at 2 depths, 0–20 and 20–40 cm. We collected biweekly samples on 12 dates during the 1992 growing season (April–September) and on 13 dates during the 1993 growing season. In each plot 5 randomly located subsamples were collected for each zonal depth during each measurement period. Soils were weighed, oven dried at 106°C for 48 h, and reweighed to determine percent water content.

Statistical Analysis

Understory data were compared among zones over time using ANOVA techniques for a randomized block design. Main effects were year and zone. Understory measurements were also analyzed each year to help explain year-by-zone interactions. Subsamples of understory density and canopy cover were averaged by zone per replicate for statistical analysis ($n = 8$ for each year). Soil water content was analyzed each year using a repeated-measures ANOVA for a randomized block design. Main effects were zone and soil depth.

All statistical analyses were performed using the Statistical Analysis System (SAS Institute 1988). Data were tested for normality using the SAS univariate procedure. Data not normally distributed were log transformed to stabilize variance. When interactions were significant, means were separated using Duncan's new multiple range test. The alpha level was set at $P < 0.05$ for statistical significance.

Diversity indices were determined for each zone using density measurements in 1992 and 1993. Hill's (1973) N1 and N2 diversity indices were used as indicators of plant diversity. The N2 index is a measure of very abundant species and the N1 index is a measure of abundant species. Hill's modified evenness ratio was used to compare relative abundances of species among zones (Ludwig and Reynolds 1988).

RESULTS

Climate Conditions and Soil Water

Water year (30 September–1 October) precipitation values were 20% below average in 1991 and 1992 at weather stations 27 and 30 km from the site. Study site precipitation in the 1992 water year totaled 21.3 cm, half of which was received in June and July 1992. The 1993 growing season was cooler and eastern Oregon received record amounts of moisture. Precipitation totals at nearby weather stations were 140% and 149% of long-term averages, respectively. Water year precipitation on the study site totaled 41.8 cm.

In 1992 soil moisture at both depths was significantly greater ($P < 0.05$) in debris zones than in interspaces from late June through September (Fig. 1). In 1993 soil water at 0–20 cm depth was significantly greater under debris than in the interspace (Fig. 1A). Except for 2 periods, mid-May and July, there were no differences in soil water content at 20–40 cm between the 2 zones in 1993 (Fig. 1B).

There were significant time-by-zone-by-depth interactions for soil water in 1992 and 1993 ($P < 0.05$). These interactions indicated that soil water decreased as the growing season progressed and was greater at both depths in the debris zone than in the interspace. Depth-by-zone ($P < 0.05$) interactions indicate that soil water was greater at 20–40 cm than 0–20 cm in the soil profile.

Understory Density and Cover

PRETREATMENT VEGETATION PATTERNS.—Perennial plant basal cover in interspace and duff locations was very low prior to the cutting treatment (Fig. 2A). Total plant basal cover did not differ between zones. However, for several species we detected significant differences in cover between zones. Basal cover of *Poa sandbergii* and *Sitanion hystrix* was greater in duff zones than in interspaces ($P < 0.05$, Fig. 2A). Basal cover of *Stipa thurberiana* was highest in interspaces ($P < 0.05$). Densities of *Poa* and *Sitanion* were greater in the duff zone than in interspaces ($P < 0.05$, Fig. 3A). Density of *Stipa*, *Agropyron spicatum*, and *Alyssum allyssioides*

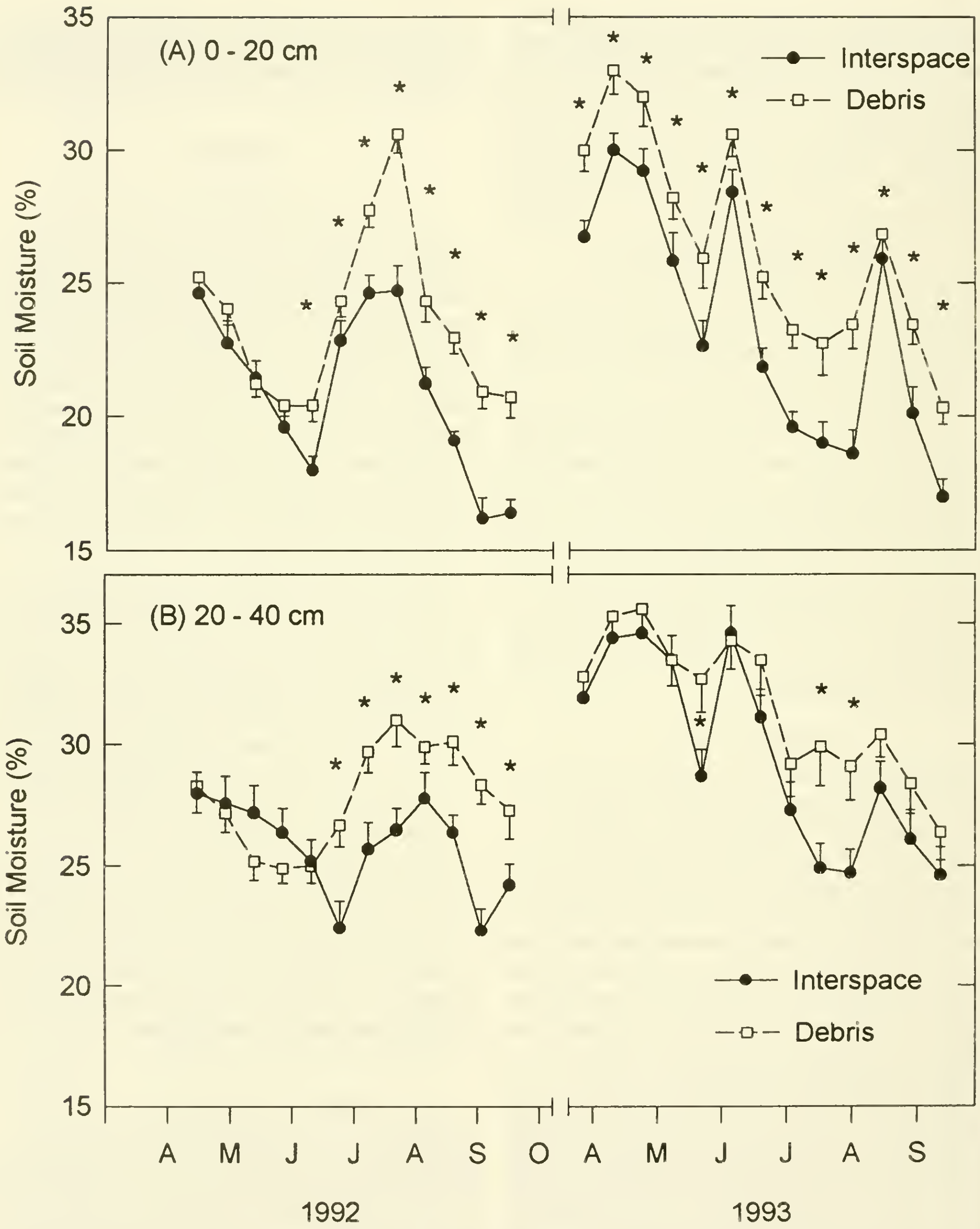

Fig. 1. Volumetric soil water content in interspace and debris zones from (A) 0–20 cm and (B) 20–40 cm depths during the 1992 and 1993 growing seasons. Data are in means ± $s_{\bar{x}}$. Asterisks (*) denote significant differences between zones ($P < 0.05$).

was greater in interspaces than in the duff zone ($P < 0.05$, Figs. 3A, 4A). Density values for annual forbs in 1991 are probably low and incomplete because sampling did not take place until July, well past the peak for annual forb growth.

POSTTREATMENT VEGETATION PATTERNS.—Cover and density of understory species differed significantly among debris, interspace, and duff zones ($P < 0.05$) after cutting (Figs. 2–4). Cover of perennial plant species and density of most other understory species

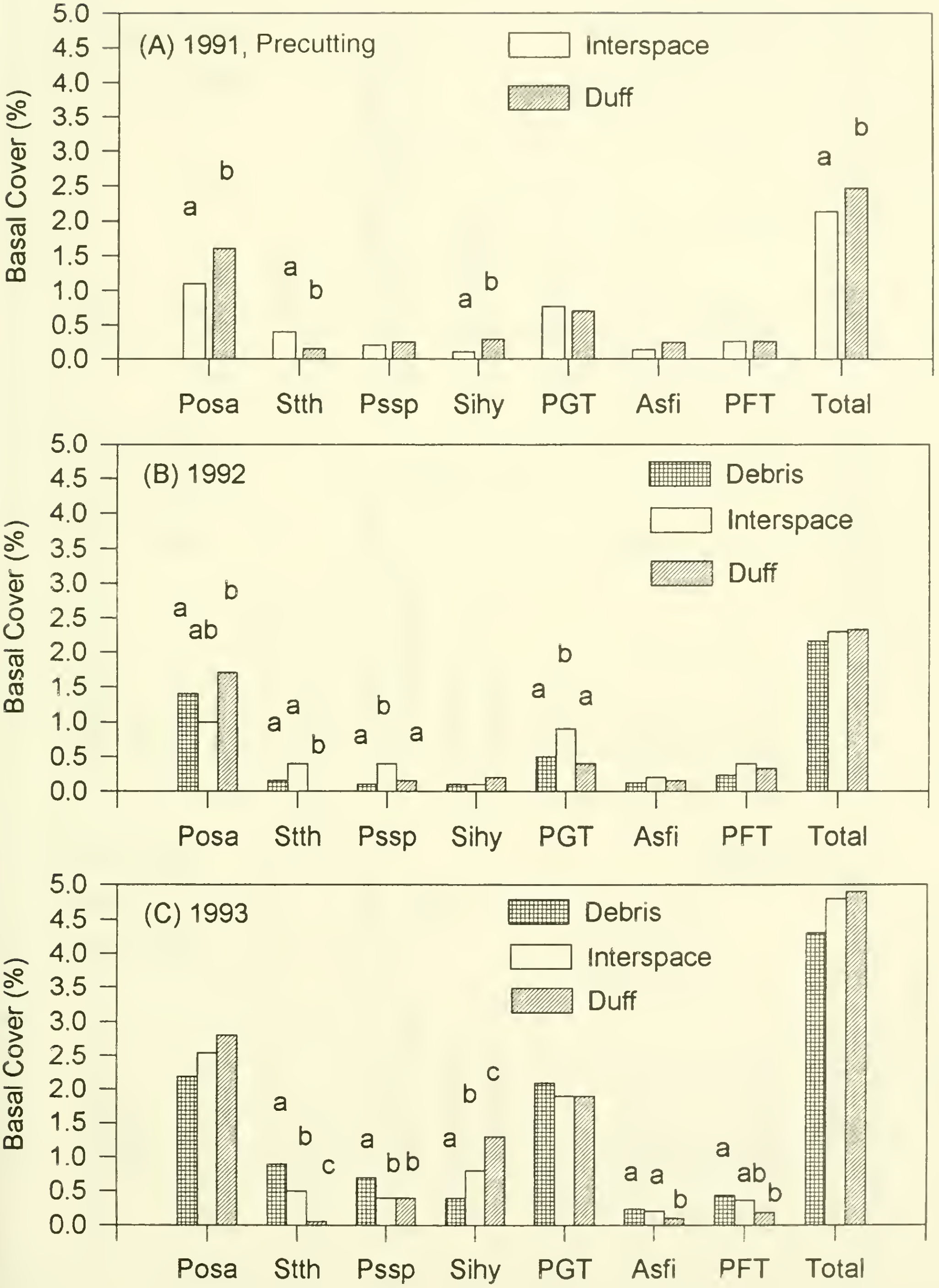

Fig. 2. Understory basal cover in (A) 1991 (precutting data), (B) 1992, and (C) 1993 for the most common perennial plants. Different letters denote significant zonal differences ($P < 0.05$) between species or plant groups. Species abbreviations: Posa–*Poa sandbergii*; Stth–*Stipa thurberiana*; Agsp–*Agropyron spicatum*; Sihy–*Sitanion hystrix*; PGT–perennial grass total; Brte–*Bromus tectorum*; Asfi–*Astragalus filipes*; PFT–perennial forb total.

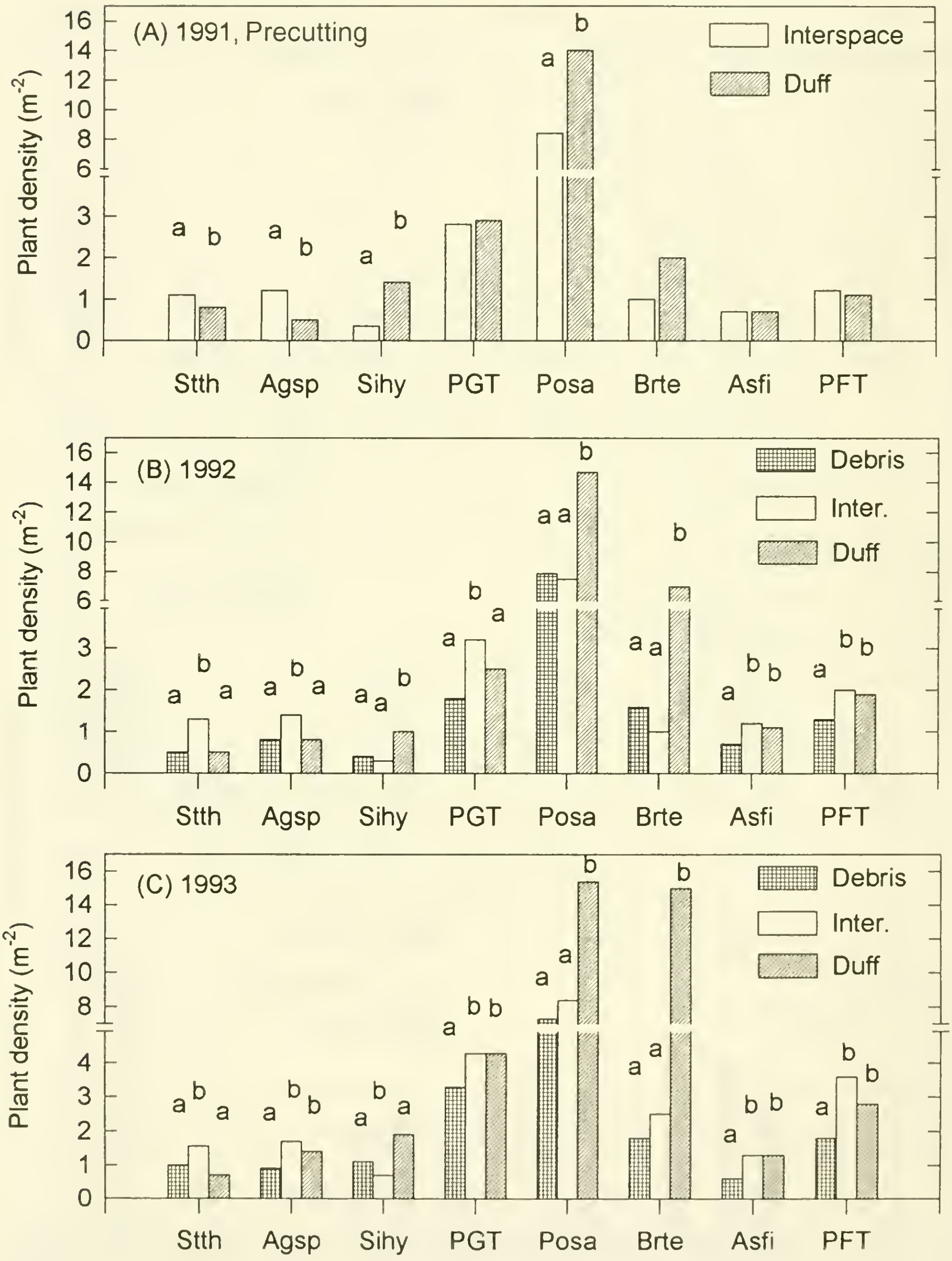

Fig. 3. Understory density in (A) 1991 (precutting data), (B) 1992, and (C) 1993 for the most common perennial plants and annual grasses. Different letters denote significant zonal differences ($P < 0.05$) between species or plant groups. Species and plant group abbreviations are defined in Figure 2.

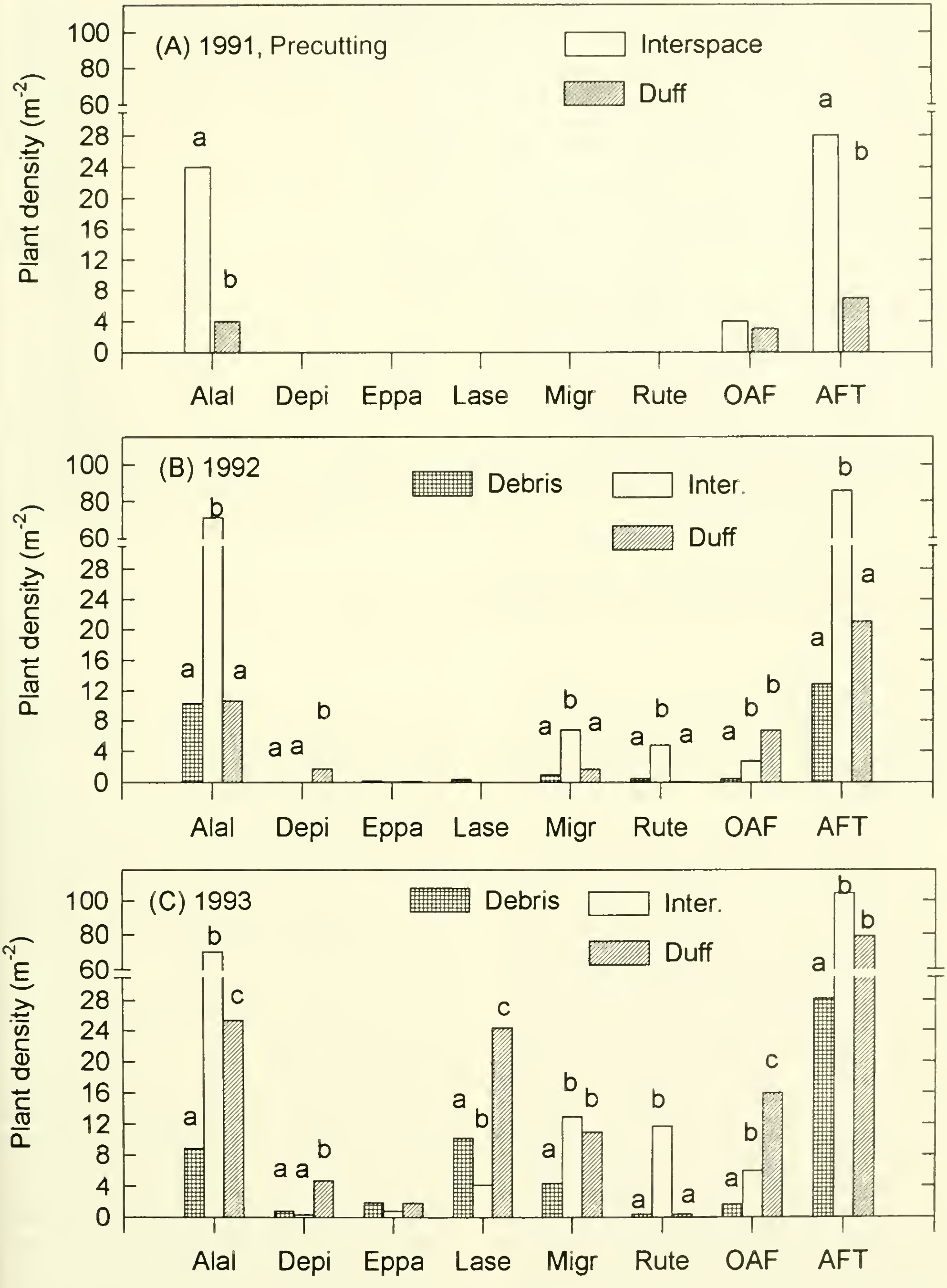

Fig. 4. Annual forb density in (A) 1991 (precutting data), (B) 1992, and (C) 1993. Different letters denote significant zonal differences ($P < 0.05$) between species and plant groups. Species abbreviations: Alal–*Alyssum alyssioides;* Depi–*Descurainia pinnata;* Eppa–*Epilobium paniculatum;* Lase–*Lactuca serriola;* Migr–*Microsteris gracilis;* Rute–*Ranunculus testiculatus;* OAF–other annual forbs (e.g., *Cirsium* spp., *Gilia* spp.); AFT–annual forb total.

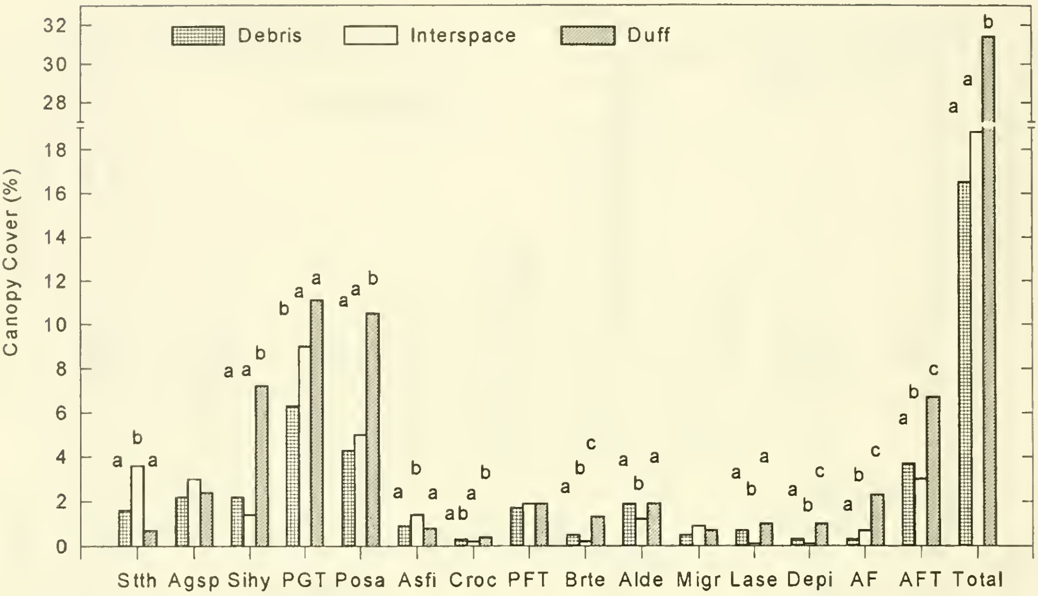

Fig. 5. Posttreatment canopy cover (%) in 1993 for interspace, duff, and debris zones. Different letters denote significant zonal differences ($P < 0.05$) among species and plant groups. New species abbreviation: Croc–*Crepis occidentalis*. Other species and plant group abbreviations are defined in Figures 2 and 4.

increased significantly between 1991 and 1993 in all zones ($P < 0.01$). Species that increased in density ($P < 0.05$) included *Sitanion*, *Agropyron*, and most perennial and annual forbs (except *Alyssum*).

Basal cover of *Sitanion*, *Astragalus filipes*, *Lomatium donnelli* (Donnell's lomatium), and perennial forbs as a group exhibited significant year-by-zone interactions ($P < 0.05$) due to an increase in basal cover in duff and debris zones between 1991 and 1993. For most species there was a lack of year-by-zone interaction indicating that plant cover and density-dominance patterns remained consistent among zones between 1991 and 1993. Basal cover (Figs. 2B,C), density (Figs. 3B,C and 4B,C), and canopy cover (Fig. 5) of *Poa*, *Sitanion*, and annual forbs remained greatest in duff compared to other zones ($P < 0.05$). Density and cover of other perennial grasses, primarily *Agropyron* and *Stipa*, and density of perennial forbs and *Alyssum* were greater in interspaces than in either duff or debris zones ($P < 0.05$).

Canopy cover and density of *Sitanion* and canopy cover of annual forbs tended to be greater in debris zones than in interspaces ($P < 0.05$). Between 1992 and 1993 basal cover of perennial grasses increased fourfold in debris zones. The change in total perennial grass cover under debris was a result of increased cover of *Sitanion*.

Groundcover also increased by the addition of juniper debris. Groundcover provided by juniper debris averaged 18% in cut plots. Together with cover provided by interspace vegetation (18%, see Fig. 5) and by old juniper litter in duff zones (22%), total groundcover after cutting was about 58% in 1993. We observed that juniper debris was effective in trapping sediment washed downslope from adjacent uncut woodlands after heavy rainstorms in July 1992.

PLANT DIVERSITY.—Diversity and species evenness tended to be greater in the duff zone in 1991 and 1992 than in the interspace or debris (1992 only) zones (Table 1). In 1993 diversity and evenness indices in both duff and debris zones were significantly greater than in the interspace ($P < 0.05$). Higher diversity and evenness ratios in duff and debris zones compared to the interspace were due to higher species richness of annual forbs and lower densities of *Alyssum* and *Microsteris gracilis*. The high densities of *Alyssum* reduced evenness and diversity in interspace zones. Plant diversity increased between 1991 and 1993 in

TABLE 1. Plant diversity (Hill's N1 and N2) and evenness ratios in interspace, duff, and debris zones. Evenness ratios in this table show a co-dominance of several species with an array of less abundant species.

Year/Location	Hill's N1	Hill's N2	Evenness
1911			
Interspace	3.1 a[1]A[2]	2.4 aA	0.5 aA
Duff	3.6 aA	2.6 aA	0.5 aA
1992			
Interspace	5.1 aB	3.5 aB	0.6 aA
Duff	7.0 bB	4.9 bB	0.6 aAB
Debris[3]	5.2 aB	3.6 aA	0.6 aAB
1993			
Interspace	5.9 aB	4.0 aB	0.5 aA
Duff	8.5 bC	6.2 bC	0.7 bB
Debris	8.7 bC	6.3 bB	0.7 bB

[1] Different lowercase letters indicate significant zonal differences in a year ($P < 0.05$).

[2] Different uppercase letters denote significant year differences within a zone ($P < 0.05$).

[3] Debris values in 1992 and 1993 are compared to 1991 interspace value because before cutting in 1991 debris zones were interspace areas.

all 3 zones ($P < 0.05$). Species evenness increased between 1991 and 1993 in debris and duff zones.

There were similarities and differences in terms of the most abundant species in each zone. Abundant species in the duff and debris zones in 1993 were *Alyssum*, *Microsteris*, *Descurainia pinnata* (pinnate tansymustard), *Lactuca serriola* (prickly lettuce), *Bromus tectorum* (cheatgrass), *Astragalus*, *Poa*, and *Sitanion*. Abundant species in the interspace were *Agropyron*, *Stipa*, *Poa*, *Alyssum*, and *Microsteris*.

DISCUSSION

Pretreatment Vegetation Patterns

Differences in understory composition between duff and interspace zones indicate that juniper influences the development of zonal microsites. Conditions in duff zones were more favorable for *Poa* and *Sitanion* than associated species, whereas conditions in the interspace favored *Stipa* and *Alyssum* (Figs. 2–5). These plant zonal patterns do not appear to be related to soil moisture content, as there were no differences detected in soil moisture availability between duff and interspace zones (Bates 1996). Duff and interspace understory patterns may be related to other factors influencing plant establishment and growth, such as temperature, light, and nutrient availability.

On warm, sunny days soil temperatures (5 cm depth) under tree canopies were 4–7°C lower than in interspaces during the growing season (1993 data, not shown). Buffering of temperature extremes beneath tree canopies may favor plants that initiate growth relatively early in the spring, such as *Poa* and *Sitanion*. Cooler temperatures under tree canopies reduce evapotranspiration (Haworth and McPherson 1995) and therefore may decrease understory water stress.

We did not measure photosynthetic active radiation (PAR) in this study, but there were indications that light levels for plant growth were reduced under canopies in duff zones in 1991. In 1991 we observed that perennial grasses tended to exhibit etiolated growth patterns in duff zones under tree canopies. Several studies have reported that as light levels decrease beneath the tree canopy with pinyon-juniper woodland development, perennial grass cover decreases (Schott and Pieper 1985, Pieper 1990). Therefore, lower light levels in duff zones than in interspaces may be responsible for lower cover and density of perennial grasses. The combination of reduced light levels and lower temperatures also reduces seed germination of annual plants (Baskin and Baskin 1985), which may explain why annual plant densities were lower in duff zones versus the interspace.

Posttreatment Vegetation Patterns

There were significant increases in understory cover, density, and diversity after juniper cutting. These increases occurred mainly during the 1993 growing season, which was characterized by more favorable growing conditions (higher spring moisture). Plant response to the cutting was limited in 1992 due to dry conditions occurring from late winter through the spring. However, the ability of the understory in the cut treatment to respond in the high precipitation year was made possible by eliminating juniper competition for soil moisture and N (Bates 1996). We believe the understory response in the cut treatment resulted from elimination of juniper competition because in adjacent uncut woodland the understory showed little response to increased precipitation in 1993 (Bates 1996).

Zonal understory plant composition did not change in duff or interspace zones after cutting. Species with greater cover (Figs. 2, 5) or density (Figs. 3, 4) in duff zones, such as *Poa* and *Sitanion*, remained dominant in the duff zone while *Stipa*, *Agropyron*, and *Alyssum* remained dominant in the interspaces. These results suggest that early postcutting understory composition, particularly for zonal dominants, is predictable based on pretreatment understory floristics. Predicting understory dynamics after cutting, however, provides only a qualitative estimate. Predicting a quantitative response is more difficult due to a number of uncertainties, particularly postcutting weather conditions. Uncertainty is also introduced by lack of knowledge about the quantity and composition of soil seed bank reserves (Koniak and Everett 1982) and the level of understory seed production following release from juniper competition. For instance, the increase in plant diversity and species richness (Table 1) in our study appears to have largely resulted from the emergence of plants from soil seed banks and belowground bulbs and tubers. Understory succession following pinyon-juniper removal by fire is also guided by initial site floristics, although prediction of posttreatment response is again limited to qualitative estimates (Everett and Ward 1984).

After cutting, plant cover increased more than did density, especially for perennial plants, because existing perennial plants grew larger in size. Between 1991 and 1993 total perennial grass basal cover increased by nearly 200%, but perennial grass densities increased by only 65% in duff zones and 43% in interspaces. The lower density response of perennial grasses was due to the lack of seed production. Except for *Sitanion*, little seed production in the perennial component was observed in 1991 or in 1992. In 1993 we observed that perennial grasses allocated a large portion of their growth to reproduction. The higher perennial seed crop in 1993 may alter plant composition on the site in subsequent years.

Litter layers in duff zones continued to influence species establishment and growth following cutting. Plant density and cover were greatest in the outer portion of the duff zone, decreasing with proximity to the tree stump where litter depth was greatest (Bates 1996). In other pinyon-juniper woodlands, plant density and cover decreased as the tree bole was approached and litter layers thickened (Everett and Sharrow 1985, Dye et al. 1995). Juniper litter may interfere with seed germination and seedling establishment by physically impeding seed-soil contact, reducing soil temperatures, and restricting plant growth via allelopathy (Jameson 1966, Peterson and Buss 1974). Although allelopathic effects should not be discounted, they seem unlikely given growth patterns of plants established in duff areas. Plants that were established or became established in the duff zone tended to grow larger than their counterparts in the interspace, particularly annual grasses and forbs.

There was a propensity for greater establishment of *Sitanion* and several annual forbs (*Lactuca*, *Cirsium* spp. [thistles]) in duff zones than in interspaces. This may be a product of seed dispersal and catchment mechanisms. Seeds of *Sitanion* and these annual forb species are typically wind dispersed. We hypothesized that old juniper needle litter in duff zones is more effective in trapping wind-dispersed seeds than the relatively bare soil surfaces characterizing the interspaces.

Juniper debris had negative and positive effects on understory plants. Prior to cutting in 1991 debris zones were interspaces. After trees were cut and debris zones created, composition of the understory shifted, developing greater similarity to duff zones than to interspace zones. In both years following juniper cutting, cover and density of *Sitanion* and the following wind-disseminated annual forbs increased under juniper debris: *Lactuca*, *Epilobium paniculatum* (willow-weed), and *Cirsium* spp. These plants tended to establish along the outer edges and less heavily shaded or open patches of the debris zone. These results indicate that microenvironmental changes can alter species composition and successional pathways.

The increase in *Sitanion* density under debris suggests that debris also may be beneficial for establishment of other grass seedlings. Once needles fall from the debris and sufficient perennial grass seed sources are available, juniper debris may serve as important microsites for other perennial grass seedlings.

Total annual forb density and cover and density of perennial grasses (except *Sitanion* and *Poa*) and perennial forbs were still significantly lower under debris than in interspaces ($P < 0.05$) in 1992 and 1993. Negative effects of juniper debris on perennial grasses (except *Sitanion* and *Poa*) and forbs were particularly evident in 1992 when compared to interspace values in 1991. Perennial grasses, such as *Stipa*, and forbs (e.g., *Astragalus*) were killed under heavy debris accumulations as evidenced by their reduced densities.

The negative impact of juniper debris on annual forbs, particularly *Alyssum* and *Microsteris*, may have resulted from lowered seed germination and/or plant establishment. Diminished light levels and lower soil temperatures due to shading by juniper debris may reduce seed germination and establishment of annual forbs, thus resulting in decreased forb density. However, annuals and perennials that did establish in debris were generally larger and stayed active longer into the season than their counterparts in the interspaces (Bates 1996).

The larger individual sizes of plants and their prolonged growing season under debris may have been a product of improved plant-water relations. Higher soil moisture levels (Fig. 1) under debris are hypothesized to have resulted from a combination of reduced evaporative loss and lower moisture demand by plants. Reduced temperatures and increased boundary layers provided by pinyon-juniper debris lower vapor pressure gradients, thereby reducing transpirational demand (Gifford and Shaw 1973). The lower density of plants under debris also may have resulted in more available resources per plant than in the interspace, thus contributing to larger plant size.

Results from this study support findings from other pinyon-juniper systems that understory plant composition is influenced by zonal location. There has been little discussion about the effects on understory zonal patterns of juniper removal by cutting, fire, or other means. Our study determined that while there were significant increases in plant cover and density resulting from juniper removal, there was little change in relative species (understory zonal dominates) composition in duff or interspace zones. Predicting qualitative species composition in duff and interspace zones, at least in the first 2 yr postcutting, is possible from pretreatment community floristics. Understory response to the deposition of juniper debris is less predictable. Changes to the microenvironment caused by juniper debris rapidly shifted understory plant composition. How juniper debris affects vegetation dynamics over a longer period of time is currently being monitored on this site. We hypothesize that overall plant community composition and development will not be radically altered by juniper debris since debris coverage averages only 18% across the site.

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COMPARATIVE DEMOGRAPHY OF THE HIGH-ALTITUDE LIZARD, *SCELOPORUS GRAMMICUS* (PHRYNOSOMATIDAE), ON THE IZTACCIHUATL VOLCANO, PUEBLA, MÉXICO

Julio A. Lemos-Espinal[1], Royce E. Ballinger[2], and Geoffrey R. Smith[3]

ABSTRACT.—Population density, reproduction, and survivorship were compared between 2 populations of *Sceloporus grammicus* occurring at different altitudes (3700 m and 4400 m) on the eastern slopes of Iztaccihuatl Volcano, Puebla, México. Lizards in both populations matured at the same age (14–15 mon) and size (39–42 mm SLV). Population density was slightly greater at high altitude (131–163 per ha) than at low altitude (52–83 per ha). Survivorship and R_0 were higher at the low-altitude area, but in general there were no significant demographic variations between altitudes that have been reported in lizard population at higher latitudes. Studies of lower-elevation populations might reveal some differences because previous studies indicate that litter size increases at lower altitudes, although they do not differ between our 3700 m and 4400 m populations.

Key words: lizard life history, demography, reproduction, altitude variation, Sceloporus grammicus, *population density, replacement rate, survivorship.*

Life histories and demographic traits of lizards can vary along elevational gradients (Ballinger 1979, Grant and Dunham 1990, Smith and Ballinger 1994a, 1994b). Altitudinal variations in life history characteristics often mimic variation observed across broader geographic ranges that can be attributed to differences in environmental conditions (e.g., Adolph and Porter 1993, 1996). In addition, some studies have shown that altitudinal variation can have at least a partial genetic basis (Smith et al. 1994, Ballinger et al. 1996), just as studies on geographic variation have shown (Ferguson and Talent 1993, Niewiarowski and Roosenburg 1993). Most of these studies have focused on lizard populations in north temperate latitudes. Understanding how life histories and demography vary in response to latitude and altitude combinations may be useful in identifying variables responsible for such changes.

In this paper we present data on demographic variation of 2 populations of *Sceloporus grammicus* Wiegmann, 1828 at different elevations (3700 m and 4400 m) to examine whether variations in demography occur at subtropical latitudes. *Sceloporus grammicus* is a small, viviparous lizard that occurs from southern Texas, USA, to the state of Oaxaca, México (Conant and Collins 1991, Flores Villela and Gerez 1994). This species has been poorly studied and little has been published on its biology, except for studies on its reproduction (Guillette and Casas-Andreu 1980, 1981, Ortega and Barbault 1984), general population biology (Lemos-Espinal and Amaya-Elias 1986), growth (Lemos-Espinal and Ballinger 1995a), and thermal biology (Lemos-Espinal and Ballinger 1995b).

MATERIALS AND METHODS

The 2 populations we studied are located in the Campo Experimental Forestal San Juan Tetla (19°10′N, 98°36′W) on the eastern slope of Iztaccihuatl Volcano, Puebla, México, at 3700 and 4400 m. On Iztaccihuatl Volcano, *S. grammicus* can be found up to 4600 m elevation. At this latitude tree line is 4000 m. The low-elevation site (hereafter designated Laguna), of approximately 4 ha, is located in a *Pinus hartwegii* forest surrounding a natural lake. Lizards were seen primarily on logs and stumps but were occasionally found under tree bark or in cracks in tree trunks. This site

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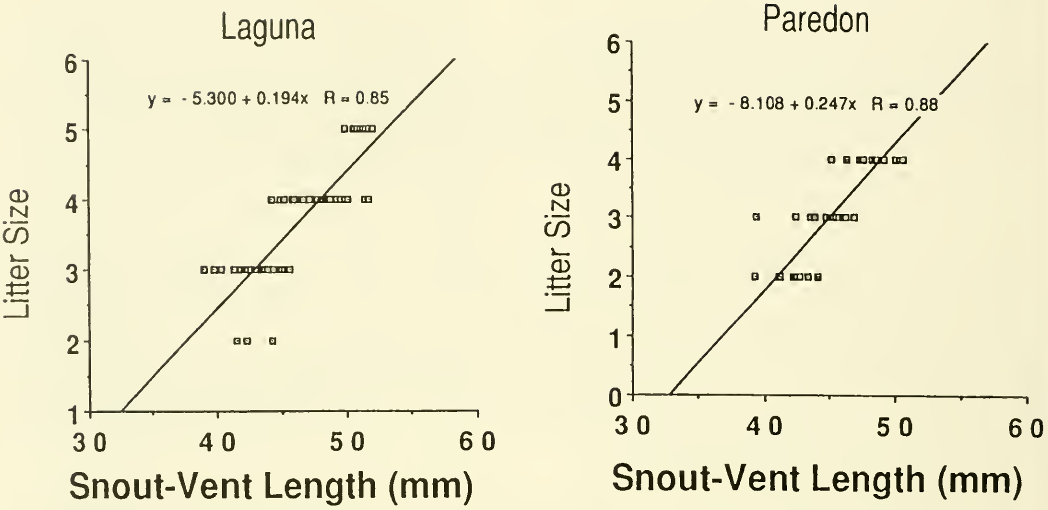

Fig. 1. Relationship of litter size to body size in pregnant *Sceloporus grammicus* from low- (Laguna) and high- (Paredon) altitude populations on the Iztaccihuatl Volcano, Puebla, México.

was studied from November 1984 to June 1988, and from September 1990 to January 1992. The high-elevation site (hereafter designated Paredon), of approximately 1 ha, is a volcanic rock formation surrounded by grassland composed primarily of *Festuca tolucensis*. Lizards at this site live under rocks and in rock crevices. We studied this site from November 1985 to June 1988, and from September 1990 to January 1992. From May 1991 to April 1992, average minimum temperatures for these 2 sites were very similar (Laguna = 2.0 ± 0.6°C [mean ± $1s_{\bar{x}}$], Paredon = 2.2 ± 0.6°C); however, average maximum temperatures for Laguna were higher (13.1 ± 0.9°C) than for Paredon (5.7 ± 0.5°C; Lemos-Espinal and Ballinger 1995a).

Both populations were censused monthly. For each captured lizard we measured snout-vent length (SVL) to the nearest mm using a clear plastic ruler, and body mass (BM) to the nearest 0.01 g using a Pesola™ spring scale. We also recorded sex, tail condition (broken, regenerated, or unbroken), time of capture, and microhabitat of capture site. Each lizard was permanently marked by toe clipping. To examine reproduction, we collected females in adjacent areas more than 500 m from the 2 study sites (n = 67 for Laguna, n = 54 for Paredon) during May 1991 and dissected them to examine reproductive tracts (specimens currently in JAL's personal collection). Size and number of yolked follicles or embryos were recorded for each female. All means are given ± $1s_{\bar{x}}$, unless specified otherwise.

Using Jolly's (1965) stochastic method, which is relatively insensitive to differences in chance of capture or survival among animals (Carothers 1973), we calculated population density for each month. Although young and old lizards may have differed in capture frequency and survivorship, bias in population estimates was probably small (Smith 1981).

Lizards were aged according to size at first capture. Since Lemos-Espinal and Ballinger (1995a) found that lizards from both study sites show the same growth rates, we used the same size categories for both populations: size class 1 (females <39 mm SVL, males <42 mm SVL; individuals in their 1st yr), size class 2 (females 39–45 mm SVL, males 42–49 mm SVL; individuals in their 2nd yr), and size class 3 (females >45 mm SVL, males >49 mm SVL; 3 yr or older). For life table analyses we estimated age by recapture of animals marked as hatchlings or by using von Bertalanffy (1957) growth analyses (Lemos-Espinal and Ballinger 1995a). Survivorship was estimated for each age class as the proportion of marked animals recaptured the following year.

RESULTS

Litter size increased with female body size in both populations (Fig. 1; r = 0.85, n = 67, P < 0.0001 for Laguna, and r = 0.89, n = 54,

$P < 0.0001$ for Paredon). Females from Laguna had significantly larger litter sizes than did females from Paredon, after controlling for differences in body size with ANCOVA (3.64 ± 0.10 [$n = 54$] vs. 3.31 ± 0.13 [$n = 67$]; $F_{1,117} = 4.92$, $P < 0.03$). The interaction term was not significant. There was no indication in our study, or in that of Guillette and Casas-Andreu (1980), that females have more than 1 litter per year.

Lizards at both study sites were born at 19–20 mm SVL. Females attained sizes of approximately 39 mm SVL by 14 mon of age (Lemos-Espinal and Ballinger 1995a). The smallest reproductive female was 39 mm SVL at both Laguna and Paredon, but an SVL of approximately 40–42 mm was the typical minimum size of reproductive females (Fig 1). These data indicate that females at both study sites mature at an age of 14–15 mon (i.e., in their 2nd fall).

Annual survivorship (l_x) was calculated for 1985–86 and 1986–87 at Laguna, and for 1986–87 at Paredon. In general, survivorship tended to be greater at Laguna than at Paredon (Fig. 2). The number of individuals per ha was greater at Paredon than at Laguna for all years of study (Table 1).

Contribution of the different age classes to age-specific fertility was similar at both study sites. Age classes 2 and 3 contributed the most (32% and 29% at Laguna, and 30% and 31% at Paredon; see Table 2). Average generation time was 3.32 yr for Laguna and 3.37 yr for Paredon. Replacement rates varied between years as did average population density (Table 2). Lower R_0 values in 1987 may have resulted because both study sites were sampled only 6 mon in 1988 (until June 1988); thus some lizards that survived from 1987 to 1988 may not have been registered.

DISCUSSION

In general, the 2 populations of S. *grammicus* studied here do not differ greatly in their biology. Survivorship estimates appear to be slightly higher in the Laguna population, but the difference is quite small. Growth rates and body temperatures also do not differ between these populations (Lemos-Espinal and Ballinger 1995a, 1995b). One of the few population differences is litter size. Females from Laguna, the low-elevation site, had slightly larger litters than did individuals from Paredon, the high-elevation site. This difference may help explain the difference in R_0 between these populations: Laguna's R_0 suggests a growing population, whereas Paredon's suggests a decreasing population. It is interesting to note that litter sizes of S. *grammicus* from lower-elevation populations (2000–3200 m) are even larger (mean = 5.2) than from our Laguna site (Guillette and Casas-Andreu 1980).

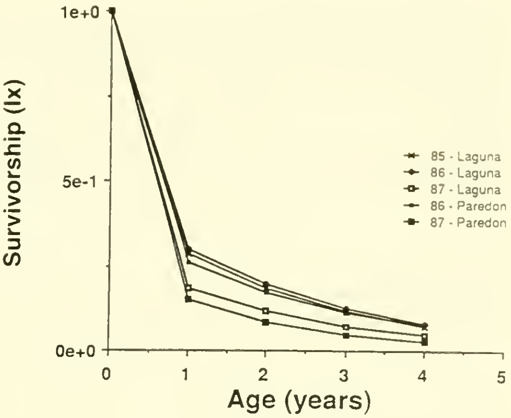

Fig. 2. Survivorship (l_x) curves for *Sceloporus grammicus* from low- (Laguna) and high- (Paredon) altitude populations on the Iztaccihuatl Volcano, Puebla, México.

The lack of major differences between these 2 populations of S. *grammicus* is in contrast to several other studies of elevational variation in life history and demographic traits, such as growth (Grant and Dunham 1990, Smith and Ballinger 1994a) and survivorship (Smith and Ballinger 1994b). While it is tempting to attribute differences between the present study and other studies to geography (i.e., differences in latitude) or elevation (present study took place at higher elevations than other studies), such a conclusion is premature. Our results, taken along with those of Guillette and Casas-Andreu (1980), do suggest there may be additional elevational differences among populations of S. *grammicus* if a broader range of elevations were studied. Our results also suggest that further studies comparing populations at different elevations from a variety of latitudes would be useful in elucidating potential causes of life history and demographic variation in lizards (and other ectotherms).

TABLE 1. Average population density for 2 populations of *Sceloporus grammicus* from the Iztaccihuatl Volcano, Puebla, México for 5 yr. Densities are given as individuals per hectare.

Population	1985	1986	1987	1988	1991
Laguna	81	79	83	52	77
Paredon	—	155	163	131	135

TABLE 2. Age-specific fertility rates ($l_x m_x$) and R_0s for low- (Laguna) and high- (Paredon) altitude populations of *Sceloporus grammicus* from the Iztaccihuatl Volcano, Puebla, México. Absolute longevity is unknown, but 5-yr-old animals have been recorded. Life table was arbitrarily stopped at the end of the 6th yr.

	Laguna				Paredon		
Age	1985	1986	1987	Mean	1986	1987	Mean
0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0
2	0.423	0.439	0.273	0.378	0.207	0.181	0.244
3	0.375	0.398	0.243	0.338	0.334	0.170	0.252
4	0.239	0.259	0.154	0.217	0.223	0.98	0.160
5	0.152	0.169	0.099	0.140	0.148	0.056	0.102
6	0.095	0.107	0.062	0.089	0.096	0.030	0.063
R_0	1.284	1.372	0.831	1.159	1.108	0.535	0.821

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NEW BISEXUAL FORM OF *CAVERNOCYPRIS SUBTERRANEA* (WOLF, 1920) (CRUSTACEA, OSTRACODA) FROM IDAHO

Okan Külköylüoğlu[1] and Gary L. Vinyard[1]

ABSTRACT.—Males of *Cavernocypris subterranea* were found for the first time in an Idaho spring. The bisexual form is described based on soft body parts and valves. The genus *Cavernocypris* now includes 2 bisexual and 1 parthenogenetic species.

Key words: Cypridopsinae, Cavernocypris subterranea, *crenobiont, bisexual form, ecology, Idaho.*

A recent revision of the genus *Cavernocypris* Hartmann (Ostracoda, Cypridopsinae) by Marmonier et al. (1989) suggested that this genus contains 3 species: *Cavernocypris subterranea* (Wolf 1920), *C. coreana* (McKenzie 1972), and *C. wardi* Marmonier, Meisch, and Danielopol, 1989. Of these, only *C. coreana* and its subspecies *C. coreana elongata* in South Korea have been reported to exist in bisexual populations (McKenzie 1972, Marmonier et al. 1989). Parthenogenetic populations of *C. subterranea* are known from Europe and central Asia, and parthenogenetic *C. wardi* has been reported from the western United States (Marmonier et al. 1989, Forester 1991, Ward et al. 1994). An undescribed species, *Cavernocypris*, n. sp., has also been reported from Arizona (Danielopol et al. 1994).

This study presents the first report of the bisexual form of *Cavernocypris subterranea* and provides the first description of males of the species.

MATERIALS AND METHODS

We collected 25 individuals (8 males and 17 females) on 4 August 1993 from Head Spring, near Brush Creek, in Malad City, Snake Valley, Bannock County (T11S, R38E, Sec 7), Idaho. Specimens were collected using a hand dipnet with a mesh size approximately 1 mm^2, preserved in 10% formalin, and subsequently stored in 70% ethanol. After isolating ostracods from the samples, we dissected specimens and mounted them in lactophenol. Species identification is based both on soft body parts and valves. Ecological and physical data collected from the collection site are shown in Table 1. All materials have been retained in the Department of Biology, University of Nevada, Reno, except for 7 specimens deposited at the Musée National d'Histoire Naturelle, Luxembourg, by Dr. Claude Meisch.

DESCRIPTION

In general, modern ostracods are described based on their soft body parts and valves. Detailed information about the terminology and more description of the parts can be found in Moore (1961) and Van Morkhoven (1962).

MALE.—Shell, viewed dorsally, is elongate and the width less than half the length. There is no double-folded inner list on the posterior margin of the left valve (LV), and LV (range, 0.67–0.73 mm) is slightly longer than the right valve (RV; range, 0.63–0.73 mm). Height (H) is less than half the length (L; range, 0.26–0.34 mm) and approximately equal to the width (W; range, 0.27–0.33 mm). In lateral view (Figs. 1A, 1B), valves are elongate and LV overlaps RV both anteriorly and posteriorly. The posterior end is slightly narrower than the anterior, but both are rounded in dorsal view. The fused zone of the inner lamella is wider at the ends and broader anteroventrally. Valves are whitish-opaque and smooth. In some European specimens the valves may have a dorsa-median band with pits. Some individuals may lack this band (C. Meisch, Luxembourg, personal

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TABLE 1. Ecological and physical data collected from the study site.

Name and location	Head Spring, Malad City, Snake Valley, Bannock County, Idaho; T11S, R38E, Sec 7
Latitude	42°48′43″ N
Longitude	112°06′09″ W
Elevation	1842 m
Water temperature	9.6°C
Conductivity	528 μS/cm
pH	7.73

communication). In our specimens decalcification has destroyed this pitted area if it was present.

The 1st antenna (Fig. 1C) or antennula (a1) has 7 segments (joints) with long natatory setae (as in females). Numbers of setae on each segment of a1 are 3:1:1–2:3:4–5:4:4. Unlike females, there is no row of delicate setae on the 1st segment of a1 of male specimens. The rome organ (r) is poorly developed.

The 2nd antenna (a2) is 4-segmented (Fig. 1D). Swimming setae of a2 on the 2nd segment are reduced to 6 small setae, 5 of which

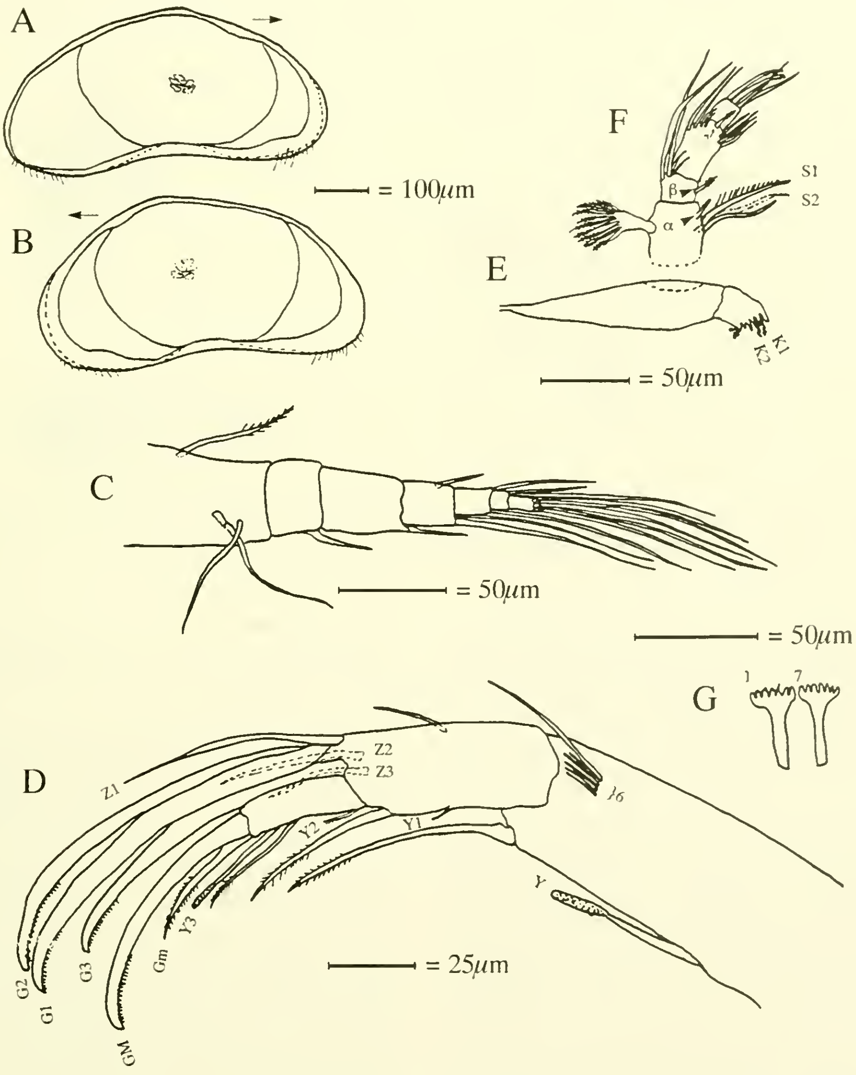

Fig. 1. *Cavernocypris subterranea*: A, left valve of male (inner view); B, right valve of female (inner view); C, 1st antenna (antennula) (a1); D, last 3 joints of 2nd antenna (a2) (2nd joint bears 5 short and 1 longer setae); E, mandibula; F, mandibular palp; G, rakelike organ with 7 teeth.

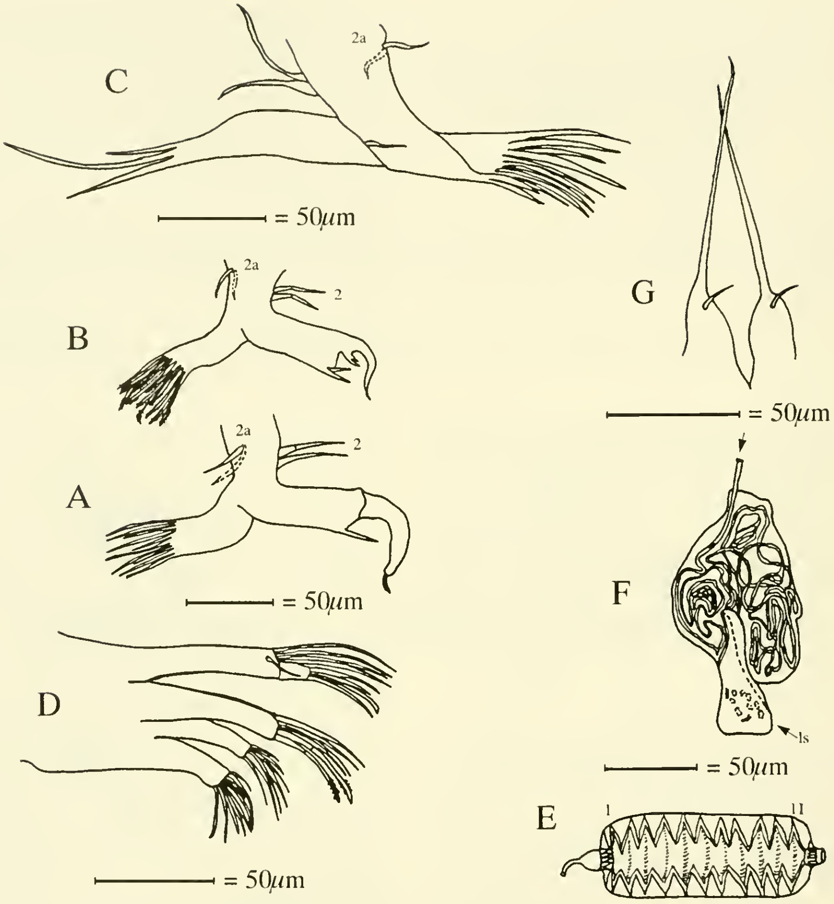

Fig. 2. *Cavernocypris subterranea*: A, maxillae of male formed as right prehensile palp and left (B) prehensile palp; C, maxillae of female in normal shape; D, maxillula and maxillular palp of male; E, Zenker organ with 11 whorls; F, hemipenis (lateral shield [ls] is spatula shaped); G, furca of female.

barely extend to the proximal margin of the penultimate joint or podomore (3rd segment). The 1st dorsally located natatory seta extends halfway up the penultimate joint (as in females). All sensory clubs "aesthetasc" (Y, y_1, y_2, y_3) are present. The aesthetasc Y is 1-segmented and its length equal to 33% of the dorsal edge of the 2nd segment and 37% of the ventral edge of the 2nd segment. The t and z setae are reduced on the 3rd segment. Claws G1 and G2 are about equal in length, 2/3 longer than G3 and 5/12 longer than the 2nd segment. Claws are serrate. Length of the GM claw on the 4th segment is about equal to G3 and 38% longer than the claw Gm that is about the same size as or slightly longer than y_3.

The mandibula (Fig. 1E) ends with 6 teeth and 3 small setae, 1 hairy and 2 smooth. There are also 2 other setae, k1 and k2. The position of k1 is between the 1st and 2nd teeth, and k2 is between the 2nd and 3rd.

The mandibular palp (Mdp) is 4-segmented with a respiratory plate (Fig. 1F). The α, β, and γ setae are present on the 1st, 2nd, and 3rd segments, respectively. The 1st segment also carries 1 long seta and S1 seta, but the S2 seta is reduced or absent. The β seta on the 2nd segment and the γ seta on the 3rd segment are feathery while the α seta is small and smooth. There are also 2 small and 2 long setae on the 2nd segment, which reach almost to the tips of the claws. The 3rd segment has 2 groups of setae, 8 total. In the 1st (dorsal) group are 2 small and 2 medium setae, whereas the 2nd (ventral) group has 4 setae, all similar in size. The 4th segment has 2 claws and 2 setae.

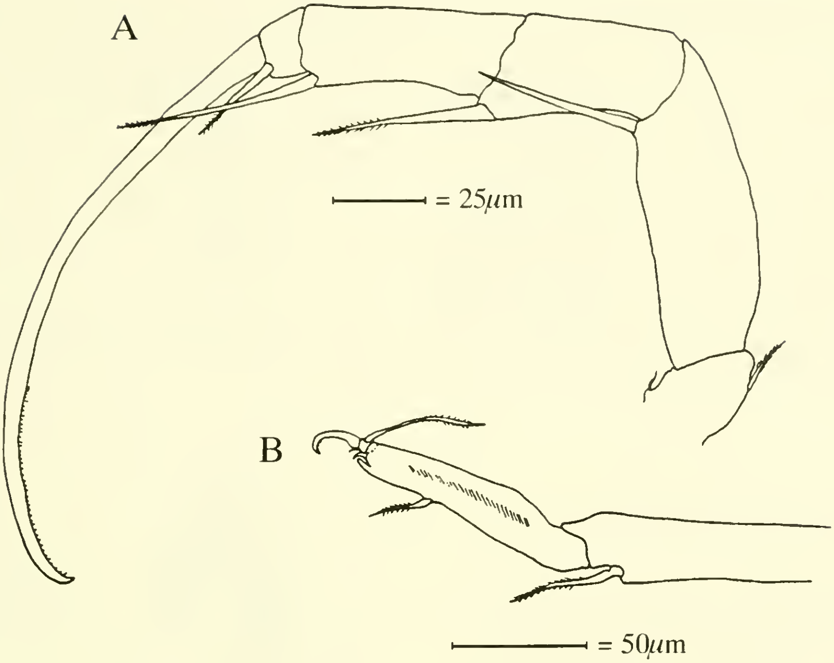

Fig. 3. *Cavernocypris subterranea* (male): A, 1st thoracopod (T1); B, 2nd thoracopod (T2).

The maxilla (Max) is formed as left and right prehensile palps with 10–12 medium-sized apical setae placed on the opposite end of the endopodite. Right prehensile palp (Fig. 2A) is slightly larger than left (Fig. 2B). The subterminal segment of the left palp has 2 small, clawlike setae (1 on the right palp). Two feathery branchial filaments are seen on the exopodite plate, a diagnostic character of the species. Two small setae (2a) are also seen on the opposite side.

The maxillula (Maxl) (Fig. 2D) bears 3 masticatory processes and 1 maxillular palp (the 4th joint). The terminal segment of the palp is rectangular in outline with 5–6 setae, 1 of which is always small. The length of the 2nd segment of the palp is twice its width. The outer (3rd) masticatory process of the maxillula has 2 spinelike setae and is scarcely toothed.

The 1st thoracopod (T1, walking leg) has a long, faintly toothed distal claw (Fig. 3A), its length nearly equal that of all 4 segments. The distal seta of the penultimate segment is long and well developed. In addition to the distal claw, the 4th segment bears 1 small seta.

The 2nd thoracopod (T2) with 4 segments is ended with 1 pincer organ, 1 well-developed seta (or 2 small setae), and 1 beaklike claw (Fig. 3B). No serrate setae occur.

A flagellum-like furca is absent in males but present in females. A small hook-shaped seta is located on the proximal part of the furca. The rake-shaped organ (Fig. 1G) is T-shaped and has 7 teeth.

The Zenker organ has 11 spinous whorls (Fig. 2E), and 1 specimen of 3 shows 3 Zenker organs rather than 2. The hemipenis (Fig. 2F) is of cypridopsine type and subtriangular in shape. The base of the lateral shield (ls) of the peniferum is straight, the medial shield rounded.

Female.—Shape and surface structure of the valves are as in males (Fig. 1B). Mean length and width of the shell of 12 females were smaller than that of males: L = 0.67–0.69 mm, H = 0.20–0.30 mm, W = 0.20–0.26 mm. A row of delicate setae is found on the 1st segment of a1. The 3rd segment has 2 setae (1 is reduced in males). Claws G1, G2, and G3 on a2 are subequal. The maxilla is shaped normally and not formed into palps (Fig. 2C). Flagellum-like furca is present (Fig. 2G). Other appendages are similar to those reported by Marmonier et al. (1989).

TABLE 2. Comparison of males of the species *C. coreana* and *C. subterranea*.

Character	*C. coreana*	*C. subterranea*
Size	0.66 mm (*elongata*) 0.72mm (*coreana*)	0.70 mm
a1	6-segment	7-segment
G3 claw	short seta	normal
t and z setae	present	reduced/absent
Aesthetasc Y	long, 2-segment	1-segment
Maxilla	with 4 filaments	2 filaments
Zenker organ	6–8 whorls (*elongata*) 8–9 or 12 (*coreana*)	11 whorls
Lateral shield	duck-head shaped	spatula shaped
Habitat	cave waters	cold springs, rivers, caves, mountain lakes

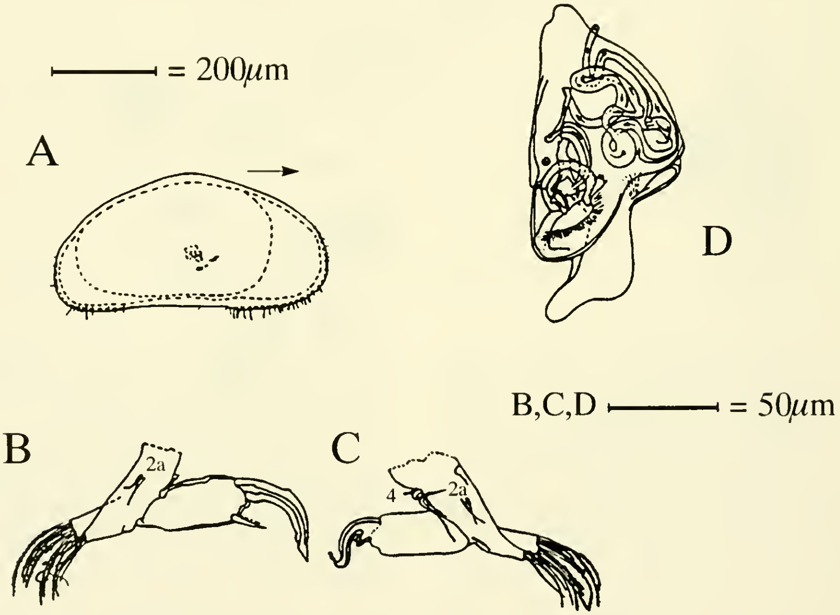

Fig. 4. *Cavernocypris coreana elongata* (male): A, right valve; B, right prehensile palp; C, left prehensile palp; D, right hemipenis, inner view (from Marmonier et al. 1989 with permission of Dr. Claude Meisch).

DISCUSSION

Determination of sexual dimorphism in *Cavernocypris subterranea* is based on the occurrence of reproductive organs and furca, size of the shell, shape of the maxilla, and differences in the length of claws (G1, G2, G3). The description of females of *C. subterranea* by Marmonier et al. (1989) also included descriptions of 2 additional species. Of these, *C. coreana* is bisexual. The males of these 2 species (Table 2) can be compared as follows: (1) *C. coreana* (Fig. 4A) is smaller than *C. subterranea*; (2) a1 is 7-segmented in *C. subterranea*, but 6-segmented in *C. coreana*; (3) the G3 claw on the antenna is reduced to a tiny, short seta in *C. coreana*, but G3 is normal and clawlike in *C. subterranea*. The t and z setae are reduced in *C. subterranea* while *C. coreana* has 2 t and 2 z setae; (4) *C. subterranea* has 2 branchial filaments on the exopodite plate of the maxilla, but *C. coreana* has 4 branchial filaments (Fig. 4B, 4C); (5) the lateral shield of the hemipenis (Fig. 4D) is duck-head shaped in *C. coreana* but spatulate shaped in *C. subterranea*; (6) Zenker organ 11 whorled in *C. subterranea*, but 8–9 whorls in *C. coreana coreana*, and 6–8 in *C. coreana elongata*, which can also bear 12 whorls (Marmonier et al. 1989). Although 1 of our specimens had 3 Zenker organs, this is considered aberrant and is not used for comparison of these 2 species. However, this characteristic may be important if the condition is found to be common. Morphological and anatomical anomalies of some freshwater ostracods (C. Meisch personal communication) were reported from Sweden and Poland after the Chernobyl accident (B. Scharf, Germany, personal communication), but the presence of 3 Zenker organs was not observed. Further studies are needed to assess causal factors for this anomaly. Habitats of these 2 species are different. *C. coreana* is known only from the cold limestone cave waters in Korea, while *C. subterranea* is crenobiont and occupies a wider range of environments including cold spring waters, river and alluvial bed sediments, caves, and the littoral zone of mountain lakes (Marmonier et al. 1989).

Based on these differences, we propose that the bisexual form of *C. subterranea* is congeneric with the bisexual forms of *C. coreana*, but not conspecific. They constitute 2 distinct species.

CONCLUSIONS

Twenty-five (8 males and 17 females) individuals of the species *Cavernocypris subterranea* were examined. The bisexual form of *C. subterranea* was found in a cold water spring in Idaho and is described for the first time. Description of the males is based on valves, soft body parts, and comparison with the other known bisexual form, *C. coreana*. Differences of morphological characters, structures, and ecological parameters indicate that males of *C. subterranea* are different from males of *C. coreana*, but the same as parthenogenetic females of *C. subterranea* found in Europe.

ACKNOWLEDGMENTS

We thank Dr. Claude Meisch (Musée National d'Histoire Naturelle, Luxembourg) for his help, comments, and encouragement as we prepared this study. Thanks are also given to Dr. Dinçer Gülen and his colleagues at the University of Istanbul (Turkey) for their comments and assistance obtaining the camera lucida, to Dr. Burkhard Scharf (Department of Inland Water Research, Germany) for personal communication, and to Robert Schroeter (University of Nevada–Reno, USA) for his review of an early draft of this manuscript.

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AN UNDESCRIBED *ASTRAGALUS* (LEGUMINOSAE) FROM SOUTHERN UTAH, A NEW SUBSECTION OF THE GENUS, AND VALIDATION OF THE COMBINATION *SPHAERALCEA JANEAE* (WELSH) WELSH

Stanley L. Welsh[1]

ABSTRACT.—One new species, *Astragalus concordius* Welsh, sp. nov., is described from Washington and Iron counties, Utah, and section *Argophylli*, subsection *Concordi* Welsh, subsect. nov., is proposed. A complete bibliographic citation is supplied to validate the nomenclatural combination *Sphaeralcea janeae* (Welsh) Welsh, Memoirs Great Basin Naturalist 9: 423. 1987.

Key words: taxonomy, Astragalus, *new species, nomenclature.*

While I was preparing keys to the species of *Astragalus* for the Flora North America project, my attention was drawn again to some peculiar plants from the Pine Valley and Kolob portions of Washington County and adjacent Iron County, Utah. Because of the peculiar leaf pubescence contrasting sharply with that of the pod, the plants will not key to any species known for Utah or Nevada in either of the previous treatments by Barneby (1964, 1989) or Welsh et al. (1987, 1993). The plants superficially resemble *A. piutensis* Barneby & Mabberley (*A. marianus* Rydberg) of section *Argophylli*, subsection *Argophylli*, and most have been identified as such. The main similarity, apart from habit, involves the long-hairy pods. However, the plants in question are appressed strigose with definitely malpighian or dolabriform pubescence, a feature not known from subsection *Argophylli* but typical of subsection *Missourienses*. Only *A. amphioxys* of subsection *Missourienses* occurs within the range of the plants in question, and that plant has merely strigose pods. Barneby (1964:697) states:

> The subsect. *Missourienses* is neatly circumscribed and defined by the presence of dolabriform hairs, but it would be hazardous to assume that it is a truly natural monophyletic group. On the contrary, it seems possible that the species have arisen independently, either singly or in pairs, from already existing *Argophylli* with basifixed vesture or from precursors of these at some remote period in the past.

Barneby (1964) then indicates examples of potential species pairs between those with basifixed and those with malpighian pubescence. Possibly this is the situation between *A. piutensis* and the new proposal. The species is, nevertheless, anomalous in any of the previously proposed subsections of section *Argophylli*.

Section *Argophylli* A. Gray

Subsection *Concordi* Welsh, subsection nov.

Similis sectione *Argophylli* subsectione *Argophylli* in legumini pubescenti sed aliter differet et similis subsectione *Missourienses* in pilis dolabriformis sed in legumini pubescenti differt.

TYPE SPECIES.—*Astragalus concordius* Welsh, sp. nov.

Subsection *Concordi* is clearly allied to section *Argophylli*, subsection *Argophylli*, with which it shares caudex features, shaggy, long-hairy pods, and general habit, but differs in the malpighian pubescence of the herbage. It shares the feature of herbage pubescence with members of subsection *Missourienses*, but not the pod pubescence.

This proposed new species has long passed under *A. piutensis* Barneby & Mabberley. Although placed in a different subsection of *Argophylli* because of contrasting pubescence types, it appears to be most closely allied to *A.*

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piutensis. The long-hairy pods of *A. concordius* are not shared by other species of subsection *Missourienses* but are known in some species in subsection *Newberryani*. In that subsection the most similar species, so far as pod pubescence is concerned, is the strictly acaulescent (not subacaulescent) *A. welshii* Barneby, which has only incipiently malpighian hairs on the herbage and differs in other regards. Welshes' milkvetch, an endemic of south central Utah (mainly on igneous gravels), is disjunct by many kilometers from the present proposal, with the nearest approach in the Black Mountain vicinity in northeastern Iron County. Relationship of subsection *Concordi* to subsection *Newberryani* appears to be tenuous.

Astragalus concordius Welsh, sp. nov.

(Fig. 1)

Similis *Astragalo piutensi* (sectione *Argophylli*, subsectione *Argophylli*) in aspectem

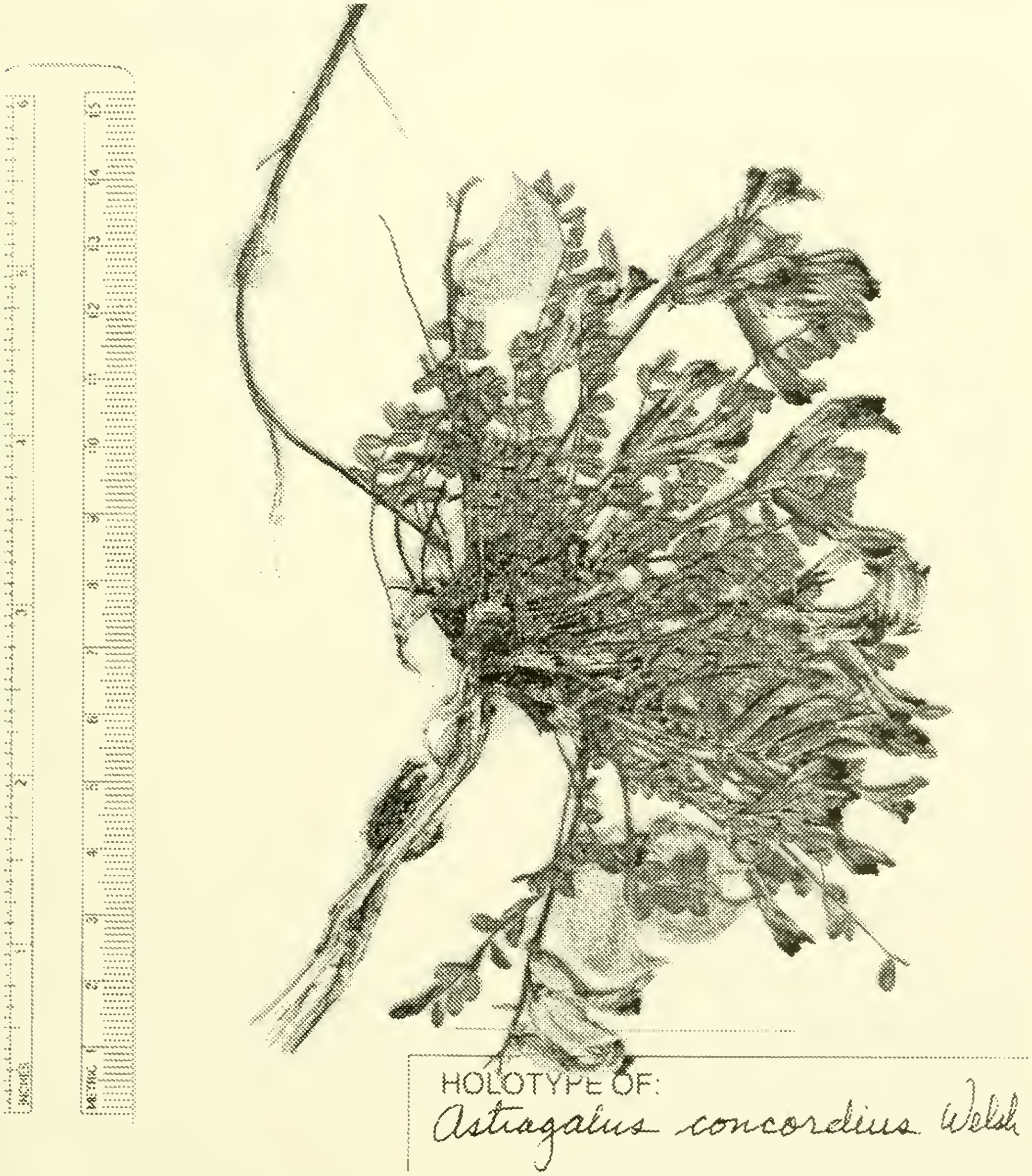

Fig. 1. Photograph of type specimen of *Astragalus concordius* Welsh.

generalem, sed pubescentis dolabriformis (nec basifixis) foliolis saepe rotundatis vel apiculatis et calyce tantum strigulosis differt.

Perennial, subacaulescent, 9–15 cm tall, from a branching caudex. **Pubescence** malpighian. **Stems** 0–6 cm long, the internodes mostly concealed by stipules, these 3.5–9 mm long, all distinct. **Leaves** 3–9 mm long; leaflets 11–17, 3.5–13 mm long, 1.2–5 mm broad, obovate to oblanceolate or elliptic, rounded to apiculate or acute, appressed strigose on both sides. **Peduncles** 1–10 cm long; racemes 2- to 8-flowered, the flowers ascending at anthesis, the axis 0.5–5 cm long in fruit; bracts 2.5–4.5 mm long; pedicels 1.5–2.5 mm long; bracteoles 0. **Calyx** 10.5–12 mm long, the tube 8.5–9.5 mm long, cylindric, strigulose, the teeth 2–3 mm long, subulate. **Flowers** 21–25 mm long, pink-purple or whitish to lilac-tinged. **Pods** spreading-ascending, sessile or nearly so, the body 15–40 mm long, 9–13 mm thick, ovoid to lance-acuminate, obcompressed, almost straight to incurved, densely shaggy-hirsute, unilocular. **Ovules** ca 30.

TYPE.—USA: Utah: Iron Co.: Flat Top Mt, ca 6 mi NE New Harmony, T37S, R12W, S31, 6200 ft elevation, 24 May 1976, S. Welsh, K. Taylor, and F. Peabody 13160a, holotype BRY (4 isotypes distributed previously as *A. marianus* Rydb.).

OTHER COLLECTIONS (PARATYPES, ALL BRY).—USA: Utah: Iron Co.: Spring Creek, SE Kanarraville, 16 May 1985, D. Atwood 11003; do, W Grants Ranch, T37S, R14W, S27, 30 May 1986, R.B. Warrick 1672; do, Upper Grants Ranch, T37S, R14W, S36, 3 June 1986, R.B. Warrick 1762. Washington Co.: along Santa Clara River, T41S, R17W, S17, 22 April 1961, A. Terril s.n.; do, E slope Pine Valley Mts, T39S, R13W, S19, 8 June 1981, D. Atwood 7901; do, 5 mi SW Enterprise Reservoir, T38S, R19W, S1, 10 June 1981, D. Atwood 9362a; do, S Kolob Reservoir, T39S, R11W, S27, 8 June 1983, L.C. Higgins & A.H. Barnum 13606; do, E slope Pine Valley Mts, T39S, R13W, 16 May 1984, D. Atwood 9652; do, Pine Spring Wash, T39S, R11W, S34, 23 April 1984, B. Franklin & G. Baird 462; do, Kolob Terrace, T39S, R11W, S34, 7 June 1948, S.L. Welsh, L. Higgins, & K. Thorne 22941; do, Pine Valley Mts, Main Canyon, T38S, R14W, S33, 2 June 1986, R.B. Warrick 1715; do, Pine Valley Mts, T38S, R13W, S9, 17 May 1986, R.B. Warrick 1379; do, Pine Spring Wash, T39S, R11W, S34, 28 May 1986, L.C. Higgins 16741; do, Horse Ranch Mt, T38S, R12W, S24, 9 July 1987, K. Thorne & S. Clark 5368; do, Kolob Plateau, T38S, R11W, S2&34, 2 July 1988, G.I. Baird 3021; do, North Creek, T40S, R11W, S34, 3 May 1988, K.H. Thorne & M.A. Franklin 6014; do, Kolob vicinity, T40S, R11W, S12, 29 April 1989, S.L. Welsh & S.L. Clark 24162; do, Hop Valley, T39S, R12W, S12, 23 May 1989, L.C. Higgins 18372.

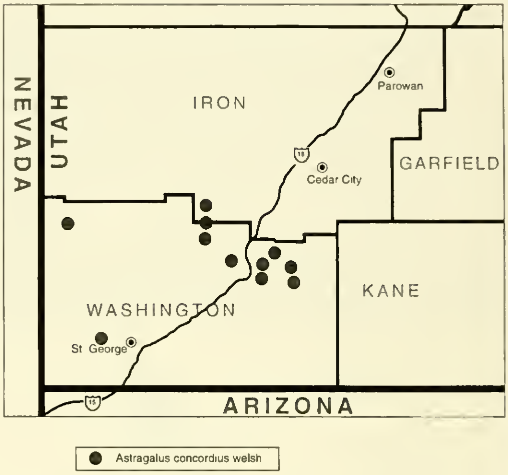

Fig. 2. Map of southwestern Utah showing distribution of *Astragalus concordius* Welsh in Washington and Iron counties.

Flowering occurs mainly during April and early May; hence most specimens are in fruit. The species occurs with ponderosa pine, manzanita, oak, aspen, mixed mountain brush, pinyon-juniper, and less commonly with Fremont poplar, willow, and ash, or rarely with creosote bush, at (1200) 1340–2600 m, mainly on sandstone or soils derived from sandstone.

Anomalous in any of the currently known subsections of *Argophylli*, *A. concordius* is most similar vegetatively, except for its malpighian hairs, with *A. pintensis*, from which it differs also in several less tangible features; i.e., leaflets are commonly rounded to apiculate, not obtuse to emarginate or acuminate; calyx is merely strigulose, not pilosulous; and at least some pods are much longer.

Distribution of the species (Fig. 2) centers in the Harmony Mountains, Iron County, Utah, and Pine Valley Mountains and Kolob Plateau regions of Washington County. The area occupied by most known collections is an oval approximately 40 km long and 20 km wide, trending along a northwest–southeast axis. Only 2 collections are known to be remote from the main body of the species, one along the Santa Clara River, ca 10 km west of the town by that name, and the other from the Bull Valley Mountains southwest of Enterprise Reservoir. The Piute milkvetch is mainly a plant of the southeastern Great Basin with only a slight overlap of distribution in the Pine Valley Mountains.

Of the numerous specimens initially considered to be *A. piutensis*, only one is from the Pine Valley Mountains; the remainder are from other Utah and Nevada localities. Thus, the 2 species are evidently disjunct, though contiguous, as are other closely related species elsewhere in the genus.

A matter unrelated to the new species of *Astragalus* was called to my attention by Dr. K.N. Gandhi, Gray Herbarium card index bibliographer, concerning the lack of proper format in what turned out to be an incomplete citation (a lapsus calamus) of *Sphaeralcea janeae* (Welsh) Welsh, published without citation of bibliographic reference of the basionym. The full citation should read, "*Sphaeralcea janeae* (Welsh) Welsh, Memoirs, Great Basin Naturalist 9: 423. 1987. [basionym: *Sphaeralcea leptophylla* var. *janeae* Welsh, Great Basin Naturalist 40: 27. 1980]." This information merely validates the earlier, intentional combination.

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AGE AND GROWTH OF JUNE SUCKER (*CHASMISTES LIORUS*) FROM OTOLITHS

Mark C. Belk[1]

Key words: June sucker, Chasmistes liorus, *age, growth, life history, otoliths, Utah Lake.*

June sucker, *Chasmistes liorus,* is endemic to Utah Lake, Utah County, Utah (Miller and Smith 1981). This species is federally listed as endangered, and the wild population may number <500 individuals (based on mark-recapture estimates, C. Keleher, Utah Division of Wildlife Resources, personal communication). The remaining *C. liorus* population appears to suffer from lack of recruitment to the adult population, apparently in part due to predation on juveniles by an abundant population of introduced white bass (*Morone chrysops*; U.S. Fish and Wildlife Service 1995). Present recovery efforts include artificial propagation. Adult *C. liorus* are captured as they proceed up the Provo River to spawn, gametes are stripped and combined, and offspring are raised in captivity until they reach a size large enough to avoid predation by white bass. These juveniles then are returned to Utah Lake, except for those retained as brood stock. To effectively evaluate survival of captive-reared individuals and to estimate age at recruitment to the breeding population, one must understand natural patterns of *C. liorus* growth in Utah Lake. Although adult size is well documented, no data are available on *C. liorus* growth patterns. In this paper I report growth pattern, size at age, and age at death of individuals estimated from presumptive annuli on otoliths (lapilli) from 10 *C. liorus* from the wild population. This study provides previously unavailable data on age and growth to serve as a baseline for comparing *C. liorus* growth patterns.

Ten *C. liorus* (7 in June 1992 and 3 in June 1994) died from unknown causes, possibly as a result of stress associated with spawning activities, and were recovered by the Utah Division of Wildlife Resources. Standard length, total length, mass, and sex were recorded for each individual. Lapilli were removed, cleaned, and embedded in epoxy resin (Serifix, Struers Corporation, Westlake, OH) for sectioning. Otoliths were sectioned in the frontal plane using a lapidary grinder (Struers Model DAP-7, Struers Corporation, Westlake, OH) and mounted on a glass slide. Thin sections were observed with a Wild dissecting microscope at 24X to determine number of annuli (age), and images were captured via a video camera mounted on the microscope and a TARGA board in the computer to measure annual increments on otoliths. Annual increments for the first 10 presumptive annuli were measured with the use of MOCHA image analysis software (Jandel Scientific Inc.). Estimated length at age was calculated using the following formula (modified Fraser-Lee method, Campana 1990):

$$L_x = L_o + (L_c - L_o)(R_x - R_o)/(R_c - R_o)$$

where L_x is estimated total length at age x, L_c is length at capture, R_x is otolith radius at age x, and R_c is otolith radius at capture. L_o is estimated length at swim-up (11 mm; Snyder and Muth 1988), and R_o is estimated otolith radius at swim-up (0.09 mm, measured from otoliths). An age-growth curve for ages 1–10 was generated by averaging back-calculated sizes at age for each sex (Fig. 1).

Estimated ages of individuals ranged from 10 to 41 yr. Two individuals had 10 presumptive annuli at death in 1992. All others had more than 25 annuli at death (Table 1). *Chasmistes liorus* exhibited a 3-stage growth pattern. Back-calculated lengths at age indicated

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TABLE 1. Presumptive age, sex, total length, year of death, and estimated total length at presumptive ages 1–10 for 10 *Chasmistes liorus*. Total lengths at ages > 10 yr were not calculated.

Presumptive age	Sex	TL	Death	Estimated total length at annulus 1	2	3	4	5	6	7	8	9	10
10	M	502	1992	87	256	355	421	461	477	492	498	501	502
10	F	526	1992	101	277	388	437	468	487	503	520	522	526
26	M	518	1992	91	259	343	380	393	414	430	449	469	470
31	F	580	1992	197	294	353	397	425	457	476	497	517	538
34	F	539	1992	149	273	302	332	351	366	390	421	434	457
35	F	568	1992	70	176	232	262	299	330	348	368	382	403
41	F	555	1992	141	204	264	320	365	395	420	438	451	455
30	F	558	1994	78	203	296	325	366	383	393	411	421	430
36	F	592	1994	97	205	251	291	327	348	373	394	405	424
37	M	502	1994	96	172	214	255	286	322	350	369	380	400
$\bar{x}$		544		111	232	300	342	374	398	418	437	449	460
s		31.7		39	45	59	64	63	60	57	54	53	49

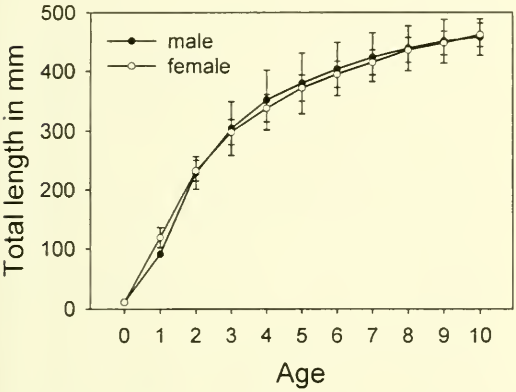

Fig. 1. Mean ($\pm 1 s_{\bar{x}}$) total length at age 1–10 for male ($n = 3$) and female ($n = 7$) *C. liorus* in Utah Lake, Utah Co., Utah, USA. Length at age calculated from presumed annual increments on otoliths. Length at ages > 10 was not calculated.

rapid growth for the first 3–5 yr, and individuals averaged 69% of mean total length at death by the 5th presumptive annulus. Following this rapid growth, individuals exhibited intermediate growth rates until about age 8–10. Eighty-five percent of mean total length at death was achieved by the 10th annulus (Table 1). Growth after age 10 was further reduced. Growth trajectories did not appear to differ between sexes within the first 10 yr, and estimated length at age 10 did not differ between sexes ($P > 0.1$, Wilcoxon rank sum test, SAS 1990; Fig. 1). Based on condition of gonads and presence in the spawning aggregation in Provo River, all individuals were reproductively mature at time of death.

Although 10 is a relatively small sample size, this sample may represent 2% of the remaining population, well above the proportion sampled in most studies on age and growth of fish. Because *C. liorus* is endangered and individuals cannot be obtained easily, validation of ages derived from otoliths has not been done. Validation of age estimates using otolith annuli has been done for other cyprinids (leatherside chub [*Gila copei*], Johnson et al. 1995; Utah chub [*Gila atraria*], unpublished data), and *C. liorus* appears to exhibit similar patterns of annulus formation. Ages derived from sectioned otoliths of *Xyrauchen texanus* have been validated for younger age classes, and ages appeared reliable for older age classes (McCarthy and Minckley 1987). However, until a validation study of ages derived from sectioned otoliths of *C. liorus* is possible, ages in this study should be considered preliminary (Beamish and McFarlane 1983).

In most fishes growth rate decreases after sexual maturity (Alm 1959). *Chasmistes liorus* examined in this study show a decreased rate of growth after about 5 annuli, and all individuals in this study were reproductively mature. Assuming that decreased growth rate indicates probable maturation, *C. liorus* may mature as early as age 5, but at least by age 10. In 1980 the smallest reproductive individuals were 440 and 490 mm total length for males and females, respectively (Shirley 1983). If growth patterns of these fish are similar to that documented in this study, then the smallest individuals likely would have been 6–10 yr old.

U.S. Fish and Wildlife Service (1995) reported total length of reproducing females was larger than males in both 1980 and 1991. Until age 10 growth patterns do not differ between sexes in this study. However, all females were larger than males, suggesting that differences in total length between sexes result from increased growth of females relative to males after sexual maturation.

C. liorus age and growth patterns appear similar to those of other large-bodied western suckers (e.g., *Chasmistes cujus*, Scoppettone 1988, Scoppettone and Vinyard 1991; *Xyrauchen texanus*, McCarthy and Minckley 1987). Delayed maturity and long adult life may be adaptations to uncertain recruitment caused by environmental fluctuations (Scoppettone and Vinyard 1991). These characteristics have allowed populations of *C. liorus* and other similar species to persist, even though recruitment has been extremely limited because of recent human disturbance. It is my hope that recovery efforts can improve recruitment before the aging adult population becomes extinct.

I thank C. Keleher and the Utah Division of Wildlife Resources, and U.S. Fish and Wildlife Service, for help in obtaining *C. liorus* otoliths. M. Lambert prepared and sectioned the otoliths. D. Shiozawa, C. Keleher, G. Scoppetone, and H. Tyus provided reviews and valuable suggestions for improvement of this note.

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RAVENS, COWBIRDS, AND STARLINGS AT SPRINGS AND STOCK TANKS, MOJAVE NATIONAL PRESERVE, CALIFORNIA

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Key words: Common Raven, Brown-headed Cowbird, European Starling, water, Mojave Desert.

We investigated use of natural and artificial water sources by Common Ravens (*Corvus corax*), Brown-headed Cowbirds (*Molothrus ater*), and European Starlings (*Sturnus vulgaris*) in the Mojave National Preserve, California. Our study was motivated by earlier observations of these 3 species in which they were seen at stock tanks but not detected at springs. Ravens, cowbirds, and starlings have been viewed as detrimental to wildlife for a variety of reasons including depredations on endangered species (e.g., desert tortoise [*Gopherus agassizii*] by ravens, Boarman 1993), nest parasitism of native songbirds by cowbirds (Trail and Baptista 1993), and competitive displacement of cavity nesting birds by starlings (Weitzel 1988, Kerpez and Smith 1990).

The Mojave National Preserve, located in San Bernardino County, California, comprises approximately 681,000 ha. It falls within an area bounded on the north by U.S. Interstate Highway 15, the east by the Colorado River, the south by U.S. Interstate Highway 40, and the west by the convergence of these 2 highways. The study area consists of mountain ranges interspersed with basins varying in elevation from 280 m to 2400 m above sea level. The climate is seasonal and severe, being warm (>26°C) in summer and cool (<11°C) in winter, with an annual mean temperature of 17 ± 9°C (*s*). Average rainfall is <12 cm for most of the area, with most precipitation occurring from December through March (Johnson 1968). Vegetation consists of widely spaced shrubs, and the major floral communities include alkali sink, creosote bush (*Larrea tridentata*) scrub, shadscale (*Atriplex confertifolia*) scrub, Joshua tree (*Yucca brevifolia*) woodland, and pinyon-juniper (*Pinus monophylla–Juniperus* spp.) woodland (Munz and Keck 1959).

Between 2 June and 5 July 1993, we sampled 60 sites consisting of 20 springs, 20 stock tanks, and 20 points located away from springs and stock tanks (controls). Springs, stock tanks, and control points were chosen from U.S. Geological Survey maps. Control points were positioned >300 m from a road and >1 km from stock tanks or springs. All points were >3 km from human habitation. Stock tanks and springs all contained open, flowing water. Stock tanks were metal or concrete structures and averaged 3 m in diameter. Controls, springs, and stock tanks were located so as to represent as broad an area as possible within the Mojave National Preserve, maximize the distance between sites, and reflect dominant regional vegetation.

Because our study examined whether bird species were associated with water, but not diurnal activity patterns, we visited sites throughout daylight hours. There were no statistical differences in time of day when the 3 site categories (springs, stock tanks, controls) were visited (Kruskal-Wallis, $\chi^2 = 3.96$, df = 2, $P = 0.14$, PROC UNIVARIATE, SAS 1987). We restricted our analyses to bird detections ≤50 m from the water points using a fixed-distance circular-plot method (Reynolds et al. 1980). We counted all detections based on either visual or aural observations during a 10-min period and recorded behavior (perched, flying, singing, feeding, drinking). Observation points were positioned so as to offer clear views of water sources. Following each count, we surveyed an area within a 50-m radius from the water source (or a designated center point for control sites) for sign (droppings, tracks, shells) of wild burros (*Equus asinus*) and domestic cows. Each site was surveyed only once.

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The total number of individuals seen during each count was used to compute means ($\pm s_{\bar{x}}$) for each species within each of the 3 site categories. A *G*-statistic (PROC FREQ, SAS 1987) was used to test for independence of species occurrences at control sites, stock tanks, and springs.

Ravens, starlings, and cowbirds were not seen equally at stock tanks, springs, and control sites ($G = 5.74$, df = 2, $P = 0.057$). Ravens and starlings were seen only at stock tanks (ravens: 1.00 ± 0.26 [$n = 20$ individuals at 12 sites]; starlings: 0.60 ± 0.41 [$n = 12$ individuals at 4 sites]). Brown-headed Cowbirds were seen at stock tanks (0.45 ± 0.29 [$n = 9$ individuals; 5 stock tanks]), were never seen at control sites, and were detected only once at springs (0.10 ± 0.07, [$n = 2$ individuals]). Of the ravens seen at stock tanks, all but 4 were seen drinking (80%). Only 17% ($n = 2$) of starlings were seen drinking and only 1 cowbird was observed drinking.

Recent evidence of cattle use was observed at all stock tanks, at 10 control sites, and at 11 springs. Burro sign was found at half of the springs, at only 2 stock tanks, and at none of the control points. One tortoise shell was found at each of 2 different stock tanks; no tortoise shells were found elsewhere.

Ravens are a species native to the Mojave though evidence suggests their populations have increased substantially, concurrent with human presence associated with linear right-of-ways, sanitary landfills, and agriculture (Knight and Kawashima 1993, Knight et al. 1993). Ravens have been implicated as a causative factor in the decline of the desert tortoise, a federally threatened species (Boarman 1993), and shells of tortoises found at stock tanks are within the size class suspected of being consumed by ravens (Boarman 1993).

Brown-headed Cowbirds did not historically occur in the east Mojave Desert (Laymon 1987). We observed groups of cowbirds, including individuals copulating, at stock tanks, whereas we detected only 2 cowbirds at a spring as they flew past. Cowbirds are stated to be associated with livestock (Mayfield 1965, Rothstein et al. 1980). Of the 7 counts at stock tanks when cows were present, we detected cowbirds only once. A more detailed study is required to document the association of cowbirds in Mojave Desert rangelands with water and livestock. If cowbird distribution in the Mojave Desert is enhanced by the presence of stock tanks, it would be worthwhile to investigate what impacts they are having on desert bird species (Laymon 1987). In the east Mojave Desert, we encountered starlings only at stock tanks or in the vicinity of homes and towns and have yet to observe them at natural water sources or undisturbed parts of the desert.

When the U.S. Congress passed the California Desert Protection Act in 1995, it rewrote the maps of southeastern California. Two national monuments (Death Valley, Joshua Tree) were made national parks, and the East Mojave National Scenic Area (U.S. Bureau of Land Management) was made an administrative unit of the National Park Service and renamed the Mojave National Preserve. Artificial water structures are allowed in Joshua Tree National Park and discouraged in Death Valley National Park; there is not yet a policy regarding water in the Mojave National Preserve. Historically, water has been viewed as a limiting factor for wildlife in much of the desert Southwest. This belief has led to a virtually unquestioned belief that if some water is good for wildlife, then more water is better (Broyles 1995). Our study hints at a possibility that there may be unanticipated costs associated with water development which, in turn, may have implications for desert wildlife communities.

Although our results are based on a single field season and within only a portion of the Mojave Desert, our findings suggest that additional research on bird communities associated with desert water sources is warranted. More detailed studies might substantiate whether the pattern we present is indeed widespread. In addition, studies that quantify bird use of different types of water, and the physical and vegetative differences associated with water types, might reveal processes that explain ecological patterns observed.

We dedicate this paper to the late Jack Kawashima, an individual who cared more than many for the integrity of the Mojave Desert. Our work was made possible by Southern California Edison and Colorado State University.

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